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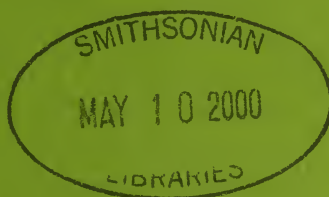
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ISOLATED VERTEBRATE COMMUNITIES IN THE TROPICS

Proceedings of the 4th International Symposium
of
Zoologisches Forschungsinstitut und Museum A. Koenig,
Bonn, May 13 – 17, 1999

Edited by
Goetz Rheinwald



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INTRODUCTION

Isolated Vertebrate Communities in the Tropics

Goetz Rheinwald

Since 1984, at intervals of five years, the Alexander Koenig Research Institute and Museum of Zoology hosts symposia on zoological problems in the tropics with a focus on Africa. The background has been described in the Proceedings volume of the first symposium (Schuchmann 1985). The first two were organized by sections of the vertebrate department and were entitled “African vertebrates: systematics, phylogeny and evolutionary ecology” (1984) and “International symposium on vertebrate biogeography and systematics in the tropics” (1989). The entomological department was responsible for the third: “International symposium on biodiversity and systematics” (1994). All Proceedings volumes are still available (see references).

This fourth symposium in 1999 was again under the auspices of the vertebrate department and was entitled: “Isolated Vertebrate Communities in the Tropics”. It was mainly organized by Dr. Renate van den Elzen.

It was the intention of the scientific staff of the department to focus on the evolutionary aspects that have led to the extreme species diversity and ecological variety so typical of the tropical biota. Since isolation is thought to be the main or even the sole precondition for the evolution of diversity, the symposium should focus on this aspect. The second idea was that evolution never takes place in individuals or isolated populations, but always in communities. So we arrived at the title of the symposium and of this volume.

We invited several speakers whose recent publications showed that they are actively working in our field of interest. More speakers were attracted by the provisional agenda, until finally we had from 13 to 17 May 1999 a symposium with 26 lectures and 20 posters. We thank all for their valuable contributions.

The topic ‘vertebrate communities’ was not absolutely adhered to in all contributions. Several papers did not fit into ‘communities’, but into ‘tropical vertebrates’. We had one presentation dealing with non-insect arthropods. Since this paper presents valuable aspects of how isolation works it is also included in this volume. We were pleased to find a speaker who supplied an introduction to phytogeography, undoubtedly the basis for all evolutionary aspects in animals. There are papers that predominantly deal with theoretical aspects, others that provide insight into biodiversity and evolutionary traits, and some that are concerned with the conservation of these isolated communities.

The contributions are arranged according to their main geographic reference. So we start in South America, and pass over West, Central and East Africa to the islands between Africa and India; we have two contributions on the Oriental region and close with two on the south of the Palearctis. Those presentations of the symposium not reported in this volume are added, with their abstracts, in alphabetical order of the authors at the end of this book.

It is my conviction that proceedings only make sense when they are published

immediately after the symposium. Therefore it was my special concern to bring together all the manuscripts in a very short time. I have to thank most contributors for their understanding on this point. Even the last ones were kind enough to ensure that the publication date was not affected.

All papers passed one or two reviewers. I am most indebted to N. Arnold – G. Arratia – A. Barker – K. Busse – R. van den Elzen – H. Enghoff – J. Fjeldså – J. Ganzhorn – J. Haffer – R. Hutterer – I. Ineich – U. Joger – M. Louette – A. Ohler – B. Patterson – G. Peters – K.-L. Schuchmann – H. Winkler, who had consideration for my desire for quick publication; nevertheless they did their job with great accuracy and responsibility, for which I thank them all sincerely. My special thanks belong to Brian Hillcoat, who very carefully went through all those papers that came from non-native English speakers. He contributed much more than only an improvement of the English. In her usual manner, S. Rick helped to solve the many large and small problems that arise with such a project.

We have to thank the great number of nameless volunteers under the guidance of A. Schunke; without their expert assistance such an international event would be impossible.

Deutsche Forschungsgemeinschaft, Bonn gave financial support in two ways: firstly DFG supplied the largest part of the budgets for the organization of the symposium (GZ 4851/34/99). In addition DFG supported the travel facilities for our East European colleagues (GZ 436 114/88/99). We thank DFG very much for this help.

Deutsche Lufthansa AG sponsored the flight of one invited speaker from abroad. **Deutsche Telekom** contributed gifts in kind for the handling of the symposium. **Stadt Bonn** gave support to persons from less developed countries.

References

- Peters, G. & R. Hutterer (1990) (eds.): *Vertebrates in the tropics. - Proceedings of the International Symposium on Vertebrate Biogeography and Systematics in the Tropics.* - Alexander Koenig Zoological Research Institute and Zoological Museum, Bonn. 424 pp.
- Schuchmann, K.-L. (1985) (ed.): *Proceedings of the International Symposium on African Vertebrates: Systematics, Phylogeny and Evolutionary Ecology.* - Zoologisches Forschungsinstitut und Museum Alexander Koenig. 585pp.
- Ulrich, H. (1997) (ed.): *Tropical Biodiversity and Systematics. - Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems.* - Zoologisches Forschungsinstitut und Museum Alexander Koenig. 357 pp.

Analyzing species composition in fragments

B.D. Patterson & W. Atmar

Abstract: Fragmented systems tend to exhibit distinctive patterns of species richness and species composition. Because local extinctions on fragments are no longer balanced by immigration from surrounding areas, their species-area relationships characteristically exhibit high slopes. Small fragments often support many fewer species than an equivalent area of contiguous habitat. In addition, fragments often support "nested subsets" of species, where the species comprising smaller local assemblages constitute a proper or included subset of the species in richer ones. Nestedness appears most prevalent and most strongly developed in fragmented systems, where species composition has been sculpted by local extinction. However, this structure also characterizes other kinds of ecological systems. Extinction, colonization, disturbance, habitat distribution, hierarchical niche relationships, and passive sampling may all shape local assemblages into nested patterns. Although nested structure *per se* can tell us little about the processes that produced it, the ordering of species and sites in a nested matrix can tell us a great deal about possible causation. Characteristics of species or sites that correlate strongly with these vectors become plausible contributors to the nested structure shown by the system as a whole.

Key words: Biogeography, extinction, habitat fragments, nested subsets, species composition

Introduction

Fragmentation of natural habitats is a progressive by-product of escalating resource consumption by humans. Continuous tracts of natural landscapes are eroded by human activities into increasingly dissected patches in an anthropogenic matrix. Fragmentation poses an especially severe threat to tropical organisms, which often have relatively small geographic ranges (Rapoport 1982, Terborgh & Winter 1983) and occur at low density because of their generally patchy distributions (Foster 1980).

Fragments differ from isolates in only one fundamental respect: their history. However, biogeographic history has pervasive effects on the types of species that are present on islands (Ricklefs & Schluter 1993, Patterson 1999; table 1). Although colonization, speciation, and extinction must simultaneously affect **all** islands continuously (at least as rates), their cumulative impact on a fauna or flora varies enormously according to its prior history.

Patterns of species richness on fragments commonly differ from those shown on isolates or in non-isolated areas of contiguous habitat. Lawlor (1986) showed that the species-area slope, z (from regressions of log species on log area), averaged twice as high in archipelagos fragmented by rising sea-levels as in oceanic ones in which islands have always been isolated. In fact, the distribution of slopes for the two classes of islands did not overlap. Smaller fragments are subject to a surfeit of

Table 1: Hallmarks of two distinctive classes of islands

	Isolates	Fragments
characteristic species	Endemics ¹⁾	Relicts
favoured species	Invaders, <i>r</i> -selected	Generalists, <i>K</i> -selected
species richness	Low species-area slopes	Steep species-area slopes
species composition	Distributional checkerboards	Nested subsets
species flux	Colonization-limited	Extinction-driven

¹⁾ Of course, endemics are also produced by vicariance, which involves fragmentation of once-continuous ranges. However, in such cases endemism arises with evolutionary divergence **after** the vicars have become isolated. The former identity of vicars (that is, as surviving daughter lineages of a widespread common ancestor that predated divergence) is underscored by the term relict. In a similar fashion, relicts may exist within currently contiguous habitats.

local extinctions as species number falls to a level commensurate with their newly circumscribed areas. Conversely, the biotas of isolates – regardless of their size – are often limited by rates of colonization (Lawlor 1986).

Historical derivation also influences the species composition of archipelagos. Many insular systems exhibit a pattern of species composition termed **nested subsets**, in which the species comprising a small fauna or flora represent a proper or included subset of those on larger, richer islands, rather than a random draw of those found in the entire species pool (Patterson 1990, Ganzhorn 1998; Wright et al. 1998). Nestedness is especially well-developed in systems thought to have undergone “faunal relaxation” (Patterson & Atmar 1986, Wright & Reeves 1992, Wright et al. 1998). During relaxation, the common species pool that occupied each island prior to fragmentation is ravaged by local extinctions until the species inhabiting the fragment are again in balance with their new surroundings (e.g., Diamond 1976). Because the extinction risk of species is often set by attributes such as body size, trophic position and habitat specialization (Brown 1971, Diamond 1984), in turn influencing their rarity, the same species tend to disappear from each of the islands, and in approximately the same order (Patterson & Atmar 1986, Blake 1991, Bolger et al. 1991, Atmar & Patterson 1993).

Nestedness is a common response to faunal relaxation, as dramatically shown by frogs on Amazonian forest fragments in the “Minimum Critical Size of Ecosystems” project (fig.1 in Wright et al. 1998; cf. Zimmerman & Bierregaard 1986). Yet most ecological systems are nested, and the factors influencing this ecological structure are as diverse as nature itself. Extinction, colonization, disturbance, habitat distribution, hierarchical niche relationships, and passive sampling may all shape local assemblages into a nested pattern (Patterson 1990, Patterson & Brown 1991, Simberloff & Martín 1991, Cutler 1994, Andrén 1994 a,b). Causes of nestedness in these specific cases are usually identified on the basis of other information available in each study. However, Lomolino (1996) proposed that causality could be assessed directly by organizing rows in the presence-absence

matrix according to each plausible determinant, and measuring the nestedness of each resulting matrix. Thus, matrices organized by area (for extinction) and by isolation (for colonization rate) could be directly compared, and the strength of these often-opposing forces could be directly assessed. However, separate analyses are required to evaluate each potential determinant (Lomolino 1996).

The Nestedness Calculator

The “Temperature Calculator” of Atmar and Patterson (1993, 1995) seems ideally suited to explore various features of nestedness, including causation. Other metrics (Patterson & Atmar 1986, Cutler 1991, Simberloff & Martin 1991, Wright & Reeves 1992, Lomolino 1996) measure nestedness in relation to the distribution of **each species**. These partial scores are then summed over species to compile community-wide patterns (i.e., counting “up” in a site \times species matrix, then summing across columns). Each ordering of rows (=sites) produces a potentially different distribution of “holes” and “outliers” and a different nestedness score.

In contrast, “temperature”, T , assesses degrees of nestedness **simultaneously across species and sites** (i.e., counting diagonally across the matrix). Just as the species compositions of fragments can be nested within one another, so too can the incidence distributions of species. Neither deserves logical precedence in ecological analyses. Moreover, there is only one arrangement of “presences” in a distribution matrix that maximizes nestedness across both these dimensions. This essential structure can then be compared to numerous possible correlates without matrix reorganization.

Atmar & Patterson (1995) developed a Windows-based Visual Basic® program for implementing analyses of T . Their “Temperature Calculator” is freely available over the Internet. Subsequent sections detail steps needed to calculate the biogeographic temperature of any set of distributions and to assess their biological determinants: (1) packing matrix elements so as to maximize nestedness; (2) measuring matrix order; (3) assessing the statistical significance of nestedness; (4) identifying and interpreting biogeographic discordance; (5) assessing causation; and (6) calculating state-occupancies.

Packing the matrix

Presence-absence matrices contain two levels of information. In addition to specifying which species occur at which sites, these matrices also reflect the relative hospitality of sites to the species under study, as well as the prevalence of environmental conditions needed to support each species. This secondary information becomes apparent only after a matrix has been packed into a state of maximal nestedness. The “hospitality” of islands or sites declines from top to bottom of the matrix. Likewise, the prevalence and width of species = niches are ordered from the left to right. Actually, these rankings of rows and columns emerge from reordering the rows and columns of the matrix to minimize the unexpectedness of occurrences.

Although few matrices prove to be perfectly nested, all matrices can be packed into a state of maximal nestedness. Matrices are packed to a condition of maximal

nestedness by reordering entire rows and columns until unexpectedness is minimized. Changing the order of rows and columns does not alter which species occur at which sites, but it does change the overall appearance of the matrix. Nested matrices can be readily distinguished without tests because their presences are tightly clustered into the upper-left corner of the matrix.

The topmost site in a packed matrix is judged the most hospitable. Similarly, the leftmost species is the one whose niche requirements are most commonly and consistently met. In practice, it may be the most resistant to extinction, most prone to colonization, or most probably encounter resources essential to species persistence.

The concept of redundancy can also be appreciated with reference to a packed matrix. When a series of sampled sites each supports all of the species in the pool, the information they provide on the ordering of species and of sites is entirely redundant. For purposes of measuring temperature and depicting matrices, such sites are combined into a single all-inclusive site in the topmost row of the matrix. For purposes of assessing the rank of individual sites (see below), all such sites are tied at first.

Calculating matrix “temperature”

The concepts of heat, information, noise, order and disorder are all closely related. The calculated metric measures the “biogeographic heat” of the matrix based on the distribution of unexpected presences and absences. In a perfectly nested matrix, the set of species on any island will be a proper or included subset of the species on all islands that precede it in the matrix. The hypothetical line that separates the occupied area of the matrix (i.e., the upper-left corner of the matrix) from the unoccupied portion is termed the **boundary line**.

The boundary line for a perfectly ordered matrix is not arbitrary nor does it depend on specific distribution patterns. Instead, the line is specified only by the size, shape, and “fill” of the matrix (i.e., how many presences it contains). Species absences above and to the left of the line are defined as **unexpected**, as are species presences below and to the right of it. Because the boundary line defines the condition of **maximal nestedness** of species and sites, every unexpected presence beyond the line is accompanied by a corresponding absence within it, and vice versa. When stochasticity is low (i.e., when T is low), unexpected presences and absences cluster near the line. As system randomness increases, the unexpected presences and absences move further away from it. The “**temperature**” of the matrix is a measure of that penetration.

Following Atmar and Patterson (1993), the formula for **local unexpectedness** of cell ij is:

$$u_{ij} = (d_{ij} / D_{ij})^2$$

where d_{ij} measures the distance of the cell from the boundary line along the skew diagonal, and D_{ij} is the length of the matrix parallel to the skew-diagonal.

Similarly, **total unexpectedness** is:

$$U = 1 / (mn) \sum \sum u_{ij}$$

summed over m rows and n columns, and **system temperature** is calculated using the constant K , where $K = 100 / U_{\max}$, as

$$T = k U.$$

Assessing probabilities

A nested distribution pattern represents a highly specific type of distribution. Monte Carlo techniques can be used to estimate the probability that the nested structure in any distribution pattern could be produced at random. To assess that probability, any number of matrices can be drawn at random to produce a baseline expectation. These matrices are generated wholly at random (i.e., 100°). However, because random events often clump together, and the matrix-packing algorithm compiles these clustered events to maximize nestedness, the randomized matrices will be cooler after they are packed. The extent to which the **characteristic temperature** of these matrices deviates from 100° depends on the size, shape and degree of fill of the matrix.

Colder characteristic temperatures will be produced in smaller matrices, those that are mostly filled or mostly empty, and in matrices that are highly rectangular (i.e., many more rows than columns, or vice versa). In each case, it is possible for the packing algorithm to cluster clumps of "presences" into the upper-left corner of the distribution matrix.

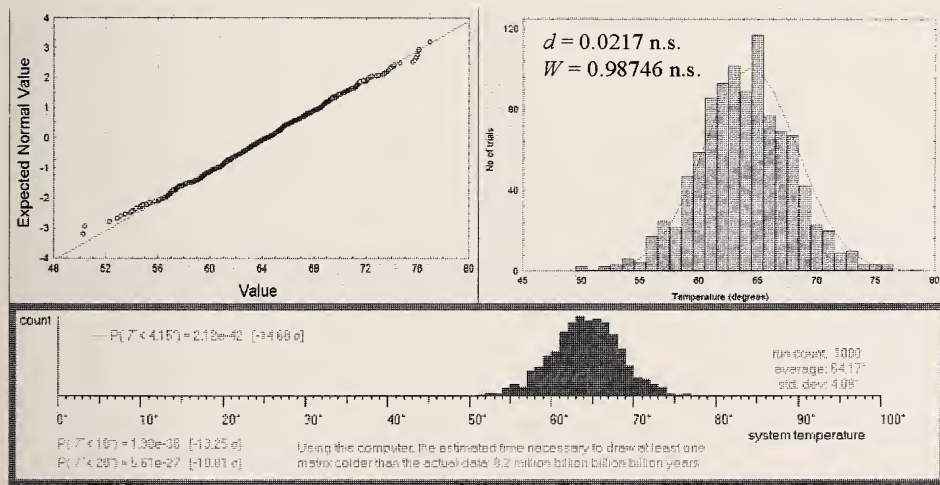


Fig.1: Testing the significance of observed nestedness. The top graphs depict tests of normality for 1000 simulation scores generated for mammals in the southern Rocky Mountain mammals (Patterson & Atmar 1986). Results of both tests for normality, the Shapiro-Wilks' W and the Kolmogorov-Smirnov d , showed non-significant differences ($P < 0.05$), validating the probability inference made in the lower graph, in which the likelihood that observed structure was part of the simulated scores is $\sim 10^{-42}$.

It then becomes a simple problem to ask “What is the probability of an observed temperature of, say 4.15° , given the trial distribution of simulated scores?” The trial distribution may be taken either as a sample of scores or as a universe. Hugueny & Guegan (1997) criticized the use of normal-probability distributions when assessing the distribution of test statistics that were generated using Monte Carlo techniques. Their argument revolved around the distribution-free nature of Monte Carlo methods, and the often-skewed distributions of test parameters. Fig. 1 contains a test for normality of 1000 temperature scores for the Rocky Mountains mammal data set of Patterson and Atmar (1986), generated using the Nestedness Calculator. Both the Shapiro-Wilks = W score and the Kolmogorov-Smirnov d test for normality are non-significant ($P > 0.05$), showing that T scores are approximately distributed as a normal variable. The result is that after measuring T in 1000 simulated archipelagos, we have far greater assurance than one in 1000 that the observed temperature of 4.15° falls outside the range of simulated scores. In fact, using a normal approximation, the probability that observed T is included within the range of simulated scores is $\sim 10^{-42}$.

Detecting idiosyncratic species and sites

Two forms of noise contribute to the temperature of a matrix: (1) the random variation of environmental, demographic, and genetic stochasticity; and (2) the “coherent” noise of specific biogeographic events or of ecologically distinctive species. Random noise creates a gray band of mixed presences and absences along the entire length of the boundary line. In contrast, coherent noise creates idiosyncratic “spikes” that correspond to species or islands that contribute much more noise than the remainder. Where temperatures are not uniformly distributed across islands and species, contrasting biogeographic histories or current ecologies are implied for those islands and species, respectively, than those that characterize the system as a whole.

Distributions of 82 species of bats along the Eastern Versant of the Andes in Peru (Patterson et al. 1996) illustrate the potential of the Calculator for identifying idiosyncrasy (fig. 2). Bat species richness falls precipitously with elevation, so that highland faunas generally represent attenuated versions of those below, forming a nested pattern. However, the individualized responses of highland bat species are strikingly discordant. Each of Manu’s endemic bat species is identified by temperature “spikes” in the lower pane of fig. 2.

Auxiliary information is required to determine why given species or islands are idiosyncratic. Idiosyncrasies often indicate unmarked heterogeneity in the original data set. Idiosyncrasies among sites may result from habitat heterogeneity (especially for groups of habitat specialists) or signify sites that experienced contrasting biogeographic histories. Idiosyncratic species might variously recolonize some islands from which they have been locally extirpated, reach their range limits in the midst of the archipelago, or be victims of competitive exclusion or products of local speciation. In this sense, idiosyncrasy may often indicate that the “rules” of the system as a whole have been violated.

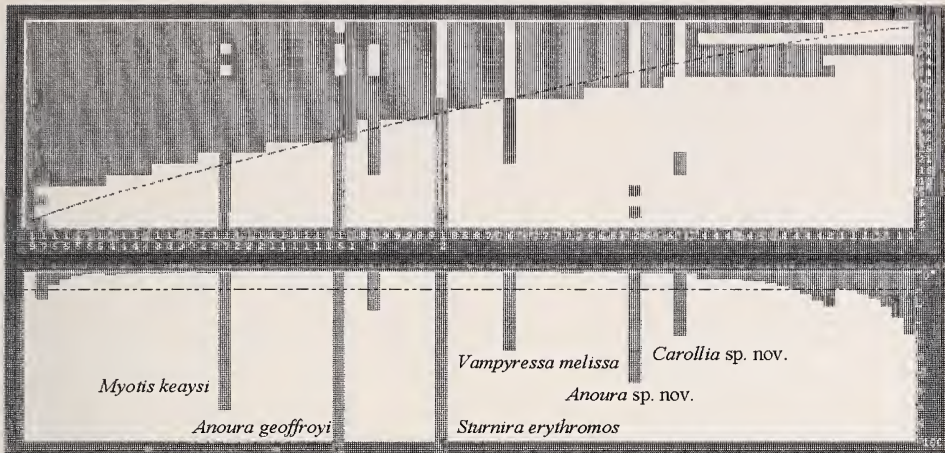


Fig. 2: Interpreting idiosyncrasies and assessing the basis for nested distributions. The upper graph shows the nested distributions of 82 bat species (columns) at 19 sampling points (rows) along an elevational gradient in the Andes in southeastern Perú (Patterson et al. 1996). In this region, species richness of bats declines rapidly with elevation, and species do not generally replace one another along the gradient; higher-elevation communities are attenuated versions of those below. The temperature of this system is 10.2° and the probability that this could be due to chance is $\sim 10^{-62}$. The lower graph shows the contrasting distributions of a handful of highland endemics, which appear as idiosyncratic “spikes” in the plot of species idiosyncrasies. The Spearman rank-correlation coefficient between rows (in the packed matrix) and elevation equals $R_s = 0.936$ ($P < 0.00001$); nested structure may be plausibly attributed to elevation (or its correlates).

Assessing causation

The existence of strongly nested distributions suggests an universal ordering mechanism for species or sites in the system under study. However, the rows and columns of the matrix submitted to analysis have been rearranged in the packing step to maximize nestedness. Where are the matrix alterations recorded, and how can matrix order be compared to independently determined features?

Matrix reorganization vectors record the rearrangements of rows and columns between matrices as submitted and those that emerged from the matrix-packing step. Descriptive vectors for either species or sites (e.g., body size estimates of species or area estimates for sites) may then be compared to the order of each in the packed matrix. Because the ordering of species by the Nestedness Calculator is only relative, rank-correlation analysis of such variables is preferred (cf. Siegel 1956).

Causal analyses are applied to two well-studied biogeographic systems. In the first (table 2), nestedness of montane mammals in the southern Rocky Mountains can be correlated with various physical features of the mountains themselves. The order of rows (mountain ranges) in the packed matrix correlates with their physical characteristics (see table) at tabulated levels. In the second, distributions of Peruvian bats over 19 sampling stations along the Eastern Versant of the Andes

Table 2: Rank-correlations of assemblages of montane mammals on mountaintops in the southern Rocky Mountains (Patterson & Atmar 1986). Row order determined by matrix packing and then correlated with various extrinsic factors.

	r_s	α
Elevation	-.327860	n.s.
Latitude	-.808813	<.00001
Longitude	.406460	<.05
Coniferous forest area	-.510545	<.01
Mesic forest area	-.678533	<.0001
Distance to source	.491228	<.05

Notes: Elevation and coordinates determined for the highest peak.

Areal measure taken from Patterson (1984), and distance measure from Lomolino et al. (1989).

are also highly nested. Correlations of row order in the packed matrix with elevation reveal strong correlation ($R_s = 0.9364$, $P < 0.0001$), suggesting that elevation or a co-variate determines nested structure. As in other non-experimental fields, causation of nestedness must be inferred from correlations and appropriate disclaimers are necessary.

Calculating state occupancy

The preceding steps for measuring nestedness apply to any matrix, regardless of its historical derivation, its current dynamics, or the uniformity of its species and sites. If more stringent assumptions of the system are warranted (such as its being at colonization-extinction equilibrium and with homogeneous resource distributions; cf. Atmar & Patterson 1993), several powerful inferences are possible.

Nested distributions imply that the cell most likely to be occupied in any matrix is the one in the upper left-hand corner; that is, the most ubiquitous species will virtually always be present on the most hospitable island. Similarly, the cell least likely to be occupied will be the bottom, right-most cell, where the most marginal species would be found on the least hospitable island. All other matrix cells vary between these extremes in a manner that is specified by their distance from the boundary line. One may therefore calculate the probability of each matrix cell being occupied. At zero degrees (the condition of perfect order), all cells within the boundary line will be filled. However, as matrix temperature increases, unexpected absences or presences begin to appear in those cells closest to the boundary line, where unexpectedness values are lowest, spreading out across the matrix as a whole.

Two graphs prepared by the Nestedness Calculator can be used to indicate the probability of a cell's occupancy. The first, a "band diagram", shows unexpectedness values for expected occurrences where the species is present, as well as unexpected presences and absences. The second, a cumulative probability diagram, shows state occupancy as a function of unexpectedness for the current matrix. It is from this second diagram that the stability of the various populations can be estimated for each cell in the matrix (fig.3). Calculating state occupancy presumes that the biogeographic noise is random rather than coherent. Thus, unexpected presences resulting from idiosyncratic causes will be deemed more unstable than they actually are. Similarly, the unexpectedness of idiosyncratic absences will be overestimated.

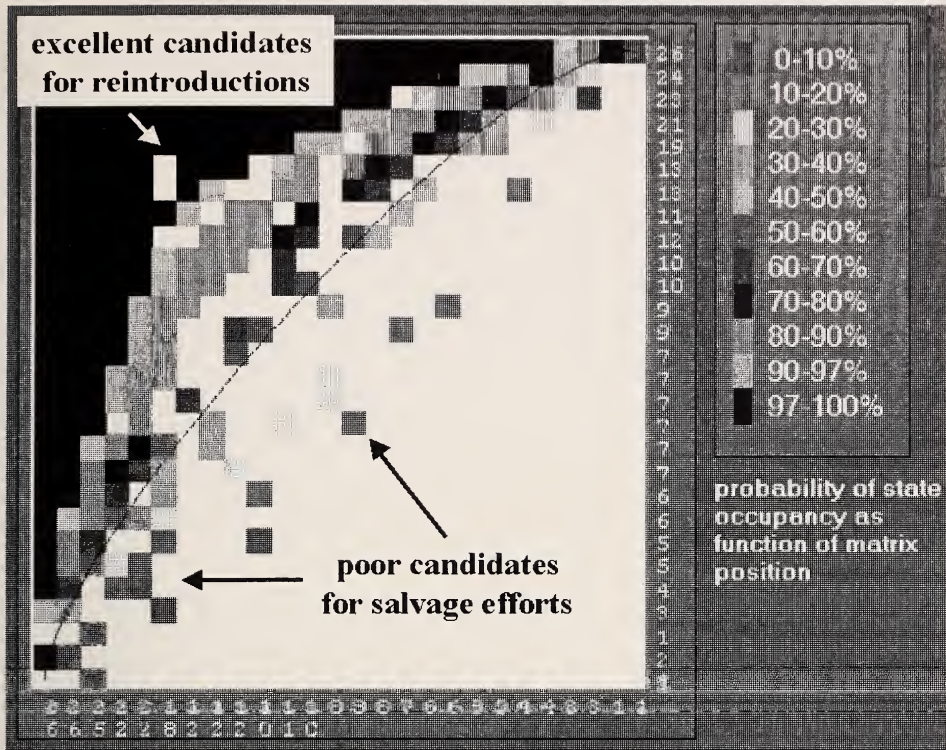


Fig. 3: Using a packed and highly nested matrix to make management decisions; data are boreal mammals of the southern Rocky Mountains (Patterson & Atmar 1986). “Holes” in the packed matrix signify populations that ought to be present, based on species co-occurrence data; introductions of such species are presumably favorable. On the other hand, “outliers” indicate populations not expected under the nested subset pattern, and seemingly a poor risk for strenuous management efforts. In fact, the lower arrow identifies an officially endangered population – *Tamiasciurus hudsonius* – on the Pinaleno Mountains, and one placed under notice of review by the U.S. Fish and Wildlife Service – *Microtus longicaudus*. Both lie outside the boundary line of nested relationships and hypothetically are next at risk of local extinction.

Discussion

Nestedness appears to be a near-universal property of the assemblages studied by ecologists and biogeographers. Its virtual ubiquity in the natural systems that scientists select for analysis is striking because, like other ecological patterns, nestedness is scale dependent (Patterson 1990). Conditions for the development of nested structure include:

- 1) the species and sites being compared must have a common biogeographic history;
- 2) both must be exposed to similar contemporary ecological conditions; and
- 3) some kind of hierarchical niche relationships among species or sites (Patterson & Brown 1991).

The first two conditions ensure that sites have been open to colonization by a common species pool. The third ensures that there are differences in the numbers of species among sites, and/or differences in the incidence of species among sites. Differences among species in extinction risk, vagility, or habitat affinities affect their incidence, whereas differences in area, isolation, elevation, or habitat composition affect the species richness of sites. Each of these variables may contribute to nested structure and deserves causal investigation.

Nestedness is a property of **assemblages**, not one of **individual species**, so it is reasonable to ask whether nestedness reveals anything that cannot be determined from the ordered distributions of constituent species (cf. Simberloff & Martin 1991). In fact, nestedness analyses can simultaneously track both overall and specific features of distributions, as illustrated in fig.2. The predominant faunal pattern shows Amazonian bat faunas becoming attenuated along the elevational gradient, with highland faunas representing nested subsets of those at lower elevations. However, the responses of a handful of highland bat species exhibit strikingly discordant patterns, as shown in the plot of idiosyncrasies. Some, such as *Sturnira erythromos* and *Anoura geoffroyi* are also perfectly ordered by elevation, only *inversely* with respect to the remaining bat species.

Nestedness requires a hierarchical ordering of sites, species or both. As widely noted (e.g., Williams 1964), habitats are often distributed in a patchy manner, and fragments may differ substantially in habitat composition, in ways affecting both species richness and composition. Sites may also be ordered with respect to isolation, area, or other variables (table 2). Orderings of species are commonly expressed in terms of niche preferences. Most biologists are familiar with the “Hutchinsonian” niche concept, based on the **probability of an organism’s survival/reproduction within a n-dimensional hyperspace**. Over all resources, this probability distribution equals the **fundamental niche**, but because other species preempt resources, the observed or **realized niche** is expressed as the occupancy of species in shared resource space. A different concept was articulated by James et al. (1984) and seems especially appropriate to geographic analyses based on presence-absence data. The “Grinnellian” niche reflects the **range of environmental values that are necessary and sufficient for a species to carry out its life history**. Within a geographic region, species occupy a geographic region congruent with the distribution of its niche. The density and incidence of species within their geographic ranges reflect the prevalence of these conditions (James et al. 1984). Seen in these terms, the rankings of species across an archipelago provide an objective ordering of species with respect to Grinnellian niche width.

Differences in incidence may influence species interactions, as detailed by Hanski (1982) in discussing core and satellite species. The nested ordering of species differs from core-satellite species mainly in being graded, not classified. A fundamental asymmetry of ecological relationships is implied by nested subsets: the “core” species in nested systems (e.g., A) are predictable elements of the environment for more marginal species (e.g., D), but the reverse is not true. Species’ responses to competition and other coevolutionary pressures should

therefore be asymmetric, with direction being set by the prevalence or incidence of the species involved. Moreover, as noted by Simberloff and Martin (1991), nested biotas are not apt to be dominated by competitive exclusion, which tends to produce distributional checkerboards, the opposite of nestedness.

Guidelines for conservation

The distinctive patterns of species richness and composition in fragments have important implications for conservation. First, the elevated slopes of species richness changes with area means that insular impoverishment with areal reduction is substantially greater on fragments than on islands (Lawlor 1986). The result is that generalized “island” slopes are inappropriate for predicting the species richness values of fragments (Patterson 1991; Doak & Mills 1994). By using such “typical” slopes, previous forecasts of tropical species loss with deforestation (e.g., Simberloff 1986) seriously underestimate the eventual costs of habitat conversion.

Nested subsets also have relevance to biological conservation, most obviously in resolving the SLOSS conundrum. In a perfectly nested archipelago, small reserves each support **the same set of species** (Patterson & Atmar 1986). However, few systems are perfectly nested, and nestedness is seldom perfectly correlated with island area. In addition, systems of small reserves, when selected on the basis of faunal or floral dissimilarity, will often preserve more species than the single largest island (Simberloff & Gotelli 1984). The utility of nestedness in reserve planning appears to be limited, at least when the compositions of all areas are known – “smart” amalgamation routines invariably perform better than those based solely on area considerations, whether from small-to-large or large-to-small (Cook 1995, Lomolino 1996).

But nested subsets have other implications as well. In any strongly nested archipelago, the boundary line marks the distributional limits of the fauna or flora, beyond which population lifetimes are expected to be nil, and species are either absent or expected to be absent. This leads to the expectation depicted in fig.4, that population lifetimes should vary systematically over a nested matrix, reaching their zenith at the origin. In general, we can expect greatest survivorship for the most widespread species on the most hospitable fragment, and declining probabilities for more narrowly distributed species and less hospitable fragments until we reach the boundary line. For a biological system that is undergoing faunal relaxation, the matrix cells distributed along the boundary line denote populations that are most at risk. For a highly dynamic biological system comprised of metapopulations, those boundary populations will wink on and off with greatest frequency, as local populations momentarily recover from local extinctions only to disappear again.

In general, rarity should be inversely correlated with population lifetimes shown in fig.4 (Diamond 1984). The precise position of the boundary line will then depend on the intensity or scale of sampling. Exhaustive sampling (that will uncover the rarest, most narrowly distributed species population in a fragment) or long-scale sampling (that uncovers and records populations that are present only episodically in a given site; cf. Andrewartha & Birch 1954) will shift the boundary line to the lower right of the matrix. This does not, however, render the nested pattern artifactual because nestedness depends on the pattern of co-occurrence, not

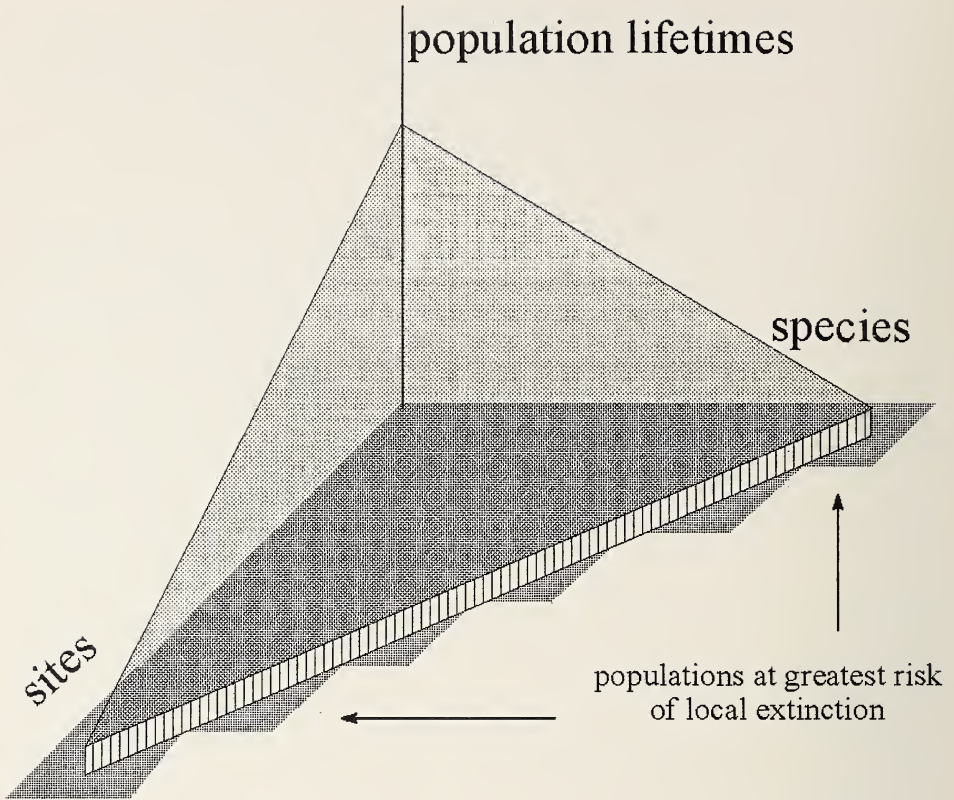


Fig.4: Hypothetical relationship between population lifetimes and the position of populations in a highly nested matrix. By definition, lifetimes fall to zero where the species is absent, but should generally increase – perhaps more-or-less regularly – as one approaches the most widespread species on the most hospitable fragment. All along the boundary line, populations of different species are thought to be most at risk.

the number of occurrences. Livingstone & Grayson (1994) showed that sampling artifacts for Great Basin mammals actually obscured the underlying nested structure, and that additional records of occurrence from more intensive sampling improved the fit of these mountaintop mammals to the nested pattern.

Nestedness is fundamentally a type of hierarchical organization. Hierarchies are familiar to biologists, forming the basis of the Linnean system of nomenclature, as well as the foundation for most attempts to classify the world's biogeographic regions. Despite their simplicity, hierarchies provide a powerful means of storing and retrieving abundant information. As one example, few people can have personal knowledge of *Pseudoryx nghetinhensis*, an animal discovered in central Vietnam in 1992. However, knowing the hierarchical position of this species (Mammalia, Artiodactyla, Bovidae, Bovinae, Boselaphini or Tragelaphini; Schaller & Rabinowitz 1995) permits a host of inferences regarding its morphology, genetics, and evolution. In a similar manner, knowledge of the hierarchical

structure of nested biotas permits numerous inferences – for example, if species M is present, then so too are species A, B, C, ..., K, and L. Although Simberloff & Martin (1991) questioned whether community-wide statistics had any transcendental value (compared to those calculated on a per-species basis), surely this predictivity is one important reason. The **relative rankings** of species and fragments and the ancillary analyses they permit provides another.

Many questions in ecology and evolutionary biology require knowledge of species-abundance relations, but nestedness analyses are based solely on presence-absence data. Although this limits the potential applications of nestedness, this feature is seen as a distinct advantage because of “data economy”. Even the most rudimentary ecological sampling yields a set of species occurring together at a place and time. Such so-occurrence data are often the best we can manage for many poorly sampled tropical areas. Moreover, given spatial and temporal variation, the presence or absence of species should be more stable than their relative abundance rankings. Development of theory that is compatible with such data should be a high priority for conservationists, again especially in the tropics. Understanding the potential biases of such analyses can only refine our ability to fashion useful predictions from them.

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References

- Andrén, A. (1994a): Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. – *Oikos* 70: 355-366.
- Andren, H. (1994b): Can one use nested subset pattern to reject the random sample hypothesis? Examples from boreal bird communities. – *Oikos* 70: 489-494.
- Andrewartha, H.G. & L.C. Birch (1954): The distribution and abundance of animals. – University Chicago Press, Chicago.
- Atmar, W., & B.D. Patterson (1993): The measure of order and disorder in the distribution of species in fragmented habitat. – *Oecologia* 96: 373-382.
- Atmar, W., & B.D. Patterson (1995): The nestedness temperature calculator: a visual basic program, including 294 presence-absence matrices. – AICS Res., Inc., University Park, New Mexico, and The Field Mus., Chicago (download at <http://aics-research.com/nestedness/tempcalc.html>).
- Blake, J.G. (1991): Nested subsets and the distribution of birds on isolated

- woodlots. – *Conserv. Biol.* 5: 58-66.
- Bolger, D.T., A.C. Alberts & M.E. Soulé (1991): Occurrence patterns of bird species in habitat fragments: sampling extinction, and nested species subsets. – *Amer. Nat.* 137: 155-166.
- Brown, J.H. (1971): Mammals on mountaintops: Nonequilibrium insular biogeography. – *Am. Nat.* 105: 467-478.
- Cook, R.R. (1995): The relationship between nested subsets, habitat subdivision, and species diversity. – *Oecologia* 101: 204-210.
- Cutler, A.H. (1991): Nested faunas and extinction in fragmented habitats. – *Conserv. Biol.* 5: 496-505.
- Cutler, A.H. (1994): Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. – *Landscape Urb. Plan.* 28:73-82.
- Diamond, J.M. (1976): Relaxation and differential extinction on land-bridge islands: applications to natural preserves. – *Proc. 16th Int. Ornithol. Congr.*, Canberra, Australia, 616-628.
- Diamond, J.M. (1984): "Normal" extinctions of isolated populations. – pp. 191-246 in: *Extinctions*. (ed. Nitecki, M.H.). – Univ. Chicago Press, Chicago.
- Doak, D.F. & L.S. Mills (1994): A useful role for theory in conservation. – *Ecology* 75: 615-626.
- Foster, R.B. (1980): Heterogeneity and disturbance in tropical vegetation. – pp. 75-92 in: *Conservation biology: an evolutionary-ecological approach* (eds. Soulé, M.E. & B.A. Wilcox). – Sinauer Assoc., Sunderland, Mass.
- Ganzhorn, J.U. (1998): Nested patterns of species composition and their implications for lemur biogeography in Madagascar. – *Folia Primat.* 69: 332-341.
- Grayson, D.K. & S.D. Livingston (1993): Missing mammals on Great Basin Mountains: Holocene extinctions and inadequate knowledge. – *Conserv. Biol.* 7: 527-532.
- Hanski, I. (1982): Dynamics of regional distribution: the core and satellite species hypothesis. – *Oikos* 38: 210-221.
- Hugueny, B. & J.F. Guegan (1997): Community nestedness and the proper way to assess statistical significance by Monte-Carlo tests: some comments on Worthen and Rohde's (1996) paper. – *Oikos* 80: 572-574.
- James, F.C., R.F. Johnston, N.O. Wamer, G.J. Niemi & W.J. Boecklen (1984): The Grinnellian niche of the wood thrush. – *Amer. Nat.* 124: 17-30.
- King, W.B. (1978-1979): *Red data book*, 2: Aves. 2nd ed. – IUCN. Morges, Switzerland.
- Lawlor, T.A. (1986): Comparative biogeography of mammals on islands. – pp. 99-125 in: *Island biogeography of mammals* (eds. L.R. Heaney & B.D. Patterson). – *Biol. J. Linnean Soc.* 28(1&2) and Academic Press, London.
- Lomolino, M.V., J.H. Brown & R. Davis (1989): Island biogeography of montane forest mammals in the American Southwest. – *Ecology* 70: 180.
- Patterson, B.D. (1984): Mammalian extinction and biogeography in the Southern Rocky Mountains. – pp. 247-293 in: *Extinctions*. (ed. Nitecki, M. H.) –

Univ. Chicago Press, Chicago.

- Patterson, B.D. (1990): On the temporal development of nested subsets patterns of species composition. – *Oikos* 59: 330-342.
- Patterson, B.D. (1991): The integral role of biogeographic theory in the conservation of tropical forest diversity. – pp. 124-149 in: *Latin American mammals: History, Biodiversity, Conservation.* (eds. Mares, M.A. & D.J. Schmidly). – Univ. Oklahoma Press, Norman, OK.
- Patterson, B.D. (1999): Contingency and determinism in mammalian biogeography: the role of history. – *J. Mamm.* 80: 345-360.
- Patterson, B.D. & W. Atmar (1986): Nested subsets and the structure of mammalian faunas and archipelagos. – pp. 65-82 in: *Island biogeography of mammals.* (eds. Heaney, L.R. & B.D. Patterson). – Biol. J. Linn. Soc. 28(1&2) and Academic Press, London.
- Patterson, B.D. & J.H. Brown (1991): Regionally nested patterns of species composition in granivorous rodent assemblages. – *J. Biogeogr.* 18: 395-402.
- Patterson, B.D., V. Pacheco & S. Solari (1996): Distributions of bats along an elevational gradient in the Andes of south-eastern Peru. – *J. Zool.* 240: 637-658.
- Quinn, J.F. & S.P. Harrison (1988): Effects of habitat fragmentation and isolation on species richness:evidence from biogeographic patterns. – *Oecologia* 75: 132-140.
- Rapoport, E.H. (1982): *Areography: geographical strategies of species.* – Fund. Bariloche Ser., Pergamon Press, Oxford.
- Ricklefs, R.E. & D. Schluter (1993) (eds.): *Species diversity in ecological communities: historical and geographical perspectives.* – Univ. Chicago Press, Chicago.
- Schaller, G.B. & A. Rabinowitz (1995): The saola or spindlehorn bovid *Pseudoryx nghetinhensis* in Laos. – *Oryx* 29: 107-113.
- Siegel, S. (1956): *Nonparametric statistics for the behavioral sciences.* – McGraw-Hill Book Co., New York.
- Simberloff, D.S. (1986): Are we on the verge of a mass extinction in tropical rain forests? – pp. 165-180 in: *Dynamics of extinction.* (ed. Elliott, D.K.) – Wiley-Interscience, New York.
- Simberloff, D.S. & N. Gotelli (1984): Effects of insularization on plant species richness in the prairie-forest ecotone. – *Biol. Conserv.* 29: 27-46.
- Simberloff, D.S. & J.-L. Martin (1991): Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. – *Ornis Fenn.* 68: 178-192.
- Terborgh, J.W. & B. Winter (1983): A method for siting parks and reserves with special reference to Colombia and Ecuador. – *Biol. Conserv.* 27: 45-58.
- Williams, C.B. (1964): *Patterns in the balance of nature.* – Academic Press, London.
- Wright, D.H. & J.H. Reeves (1992): On the meaning and measurement of nestedness of species assemblages. – *Oecologia* 92: 416-428.

- Wright, D.H., B.D. Patterson, G. Mikkelsen, A.H. Cutler & W. Atmar (1998): A comparative analysis of nested subset patterns of species composition. – *Oecologia* 113: 1-20.
- Zimmerman, B.L. & R.O. Bierregaard (1986): Relevance of the equilibrium theory of island biogeography and species-area relations to conservation with a case from Amazonia. – *J. Biogeogr.* 13: 133-143.

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Chronology and mode of speciation in the Andean avifauna

J. García-Moreno & J. Fjeldså

Abstract: This paper reviews speciation studies of Andean forest birds, using mtDNA sequence data, and explores possible driving mechanisms. Typical biogeographic patterns in the Andean forest zones comprise sharp (parapatric) replacements along the Andes and elevational replacements where species sometimes occupy different ecological zones along several thousand kilometers of Andean slopes. The DNA data (if we accept the existence of a molecular clock) reveal much variation in the timing of speciation events: the diversification has proceeded during the entire uplift of the northern Andes, with speciation in the Pleistocene glacial periods only in some lineages. Some parapatric replacements may have been maintained since before the onset of major glaciations. This suggests that vicariant forms are valid species which remain ecologically incompatible for long periods, possibly because they are subject to uniform selection pressures. Establishment of sympatry (through dispersal) may be long delayed, partly because sharp geographical replacements are maintained by physical barriers (such as a valley deeply intersecting the cloudforest zone). We suggest that most Andean species originate as relict populations which persist because of local orographic protection against ecoclimatic disturbance. The process of relictuation, which may be related to high levels of local community drift in large parts of the region, affects only some species. It therefore does not follow a consistent chronology across lineages. In order to assess whether relict taxa are recruited into the regional species pool we now need detailed studies using broader sample schemes and statistical documentation of historical community structures based on coalescence theory.

Key words: speciation, Andes, avifauna, mtDNA

Introduction

By comparing regional patterns of species richness of tropical birds representing recently radiated groups with those representing deep lineages, Fjeldså (1994) and Roy et al. (1997) demonstrated that in the recent geological past the cradle of new species was in the montane regions. The biodiversity of the South American lowland rainforest is to a large extent a legacy from the Tertiary "super-rainforest" (Hooghiemstra & van der Hammen 1998, Flenley, in press). In such lowland areas, the biogeographic signals concerning initial speciation events are buried by subsequent redistribution, and the variation in endemism reflects that of species richness and current ecology (Fjeldså et al. in press). In the montane areas, in contrast, distinctive patterns of endemism are more likely to reflect recent historical isolations (Fjeldså 1995). In this paper we will evaluate questions about the causes and mechanisms of rapid diversification in South American montane areas.

Speciation in montane areas is often explained by the many isolating barriers and the tremendous elevational gradients, where selective pressures on birds vary over

short distances (Vuilleumier 1969, 1984a, Simpson-Vuilleumier 1971, Fjelds  1992, O'Neill 1992). Attention is also given to the temporary isolation caused by Pleistocene glaciation, although this is often limited to the most recent (and best documented) glacial cycles (e.g., Vuilleumier & Simberloff 1980, Traylor 1985, Fjelds  1992, Heindl & Schuchmann 1998). These interpretations need to be re-evaluated in the light of new kinds of palaeoclimatological data and new insights into the mechanisms which drive global climatic change (see Andersen & Borns 1994 for a review). The global climate is subject to continuous orbital forcing, resulting in frequent but slight oscillations throughout the upper Tertiary, a marked cooling and longer (40 000-year) cycles in the early Pleistocene, and an abrupt change only 800 000 years ago to a period characterized by long (100 000 year) large-amplitude cycles (Hooghiemstra et al. 1993). Thus, if biological diversification were driven by periodic isolation of fragments of once-continuous biomes (Haffer 1997), and if new species were efficiently redistributed in the intervening periods, we would predict an exponential increase in speciation events in the upper Pleistocene. However, speciation could also be driven by high local biotic turnover (community drift, Hubbell 1999), which is caused by ecoclimatic disturbances on any time scale. We assume that this is possible because some species will persist only as relict populations in places which are inherently stable and where the biotic turnover is slight. Using a long series of satellite images, Fjelds  et al. (1999) were able to document that peaks of endemism in the Andes correspond to places where the interannual variability in surface conditions is slight, reflecting local orographic moderation of the climate.

As traditional ideas about processes and kinds of isolating mechanisms are currently being questioned, the understanding of processes underlying the diversification of tropical biota remains a hot topic. Rather than entertaining plausible but unfalsifiable scenarios we need clear conceptual models which allow robust testing. Lynch (1988) asked for documentation of consistent hierarchies of phylogenetic branching patterns across many taxonomic groups. However, if the diversification process was dominated by divergence of relict populations or was randomized over time, as suggested above, then only some species would be affected, and not necessarily at the same time. The predictions would then be that speciation patterns are non-synchronous in time (across lineages), that speciation was allopatric (by isolation of relict populations) and that endemism is locally aggregated. If speciation involves persistence of relict populations where the climate is predictable and the level of faunal turnover is slight, then neutral genetic drift would dominate, resulting in random variation in phenotypes between isolates.

In this paper we will review a number of case studies of Andean birds where molecular data were used. We will use these data to evaluate the ideas outlined above.

Materials and methods

We studied several widespread and species-rich groups of Andean birds, focusing on groups which show linear arrangements of species along the upper eastern Andean slope. This focus is based on the following rationale: Because of the

linearity of the band of humid montane forest (Graves 1988), we presume that sister-group relationships are mainly one-dimensional in space (and therefore easy to analyze). Populations which replace each other along the Andes, in a specific ecological zone, would also be subject to rather uniform selection pressures. It is already well documented that such groups often exhibit a 'checkerboard' variation of phenotypes, as different characters vary independently between populations, sometimes in a way which produces decided 'leapfrog' patterns (e.g., Rensch 1929, Remsen 1984a, Remsen & Graves 1995 a,b, Graves 1980, 1982, Maijer & Fjeldså 1997). Most groups also include species which replace each other sharply in different elevational zones, or on humid slopes and adjacent rainshadow slopes. This means that there will also be cases of consistent directional selection, which might cause extremely rapid phenotypic change (Carson 1990, Walter & Paterson 1994, Smith et al. 1997).

DNA was extracted from preserved blood and tissue samples. Fragments of the mitochondrial cytochrome b and/or ND2 genes were amplified and sequenced following standard protocols. The two genes exhibit similar substitution rates (Johnson & Sorensen 1999). We constructed phylogenies for those genera for which we had a good taxonomic sampling: *Atlapetes* brushfinches (García-Moreno & Fjeldså 1999), *Metallura* hummingbirds (García-Moreno et al. 1999a), *Cranioleuca* spinetails (García-Moreno et al. 1999b), various tanagers (*Hemispingus*, *Iridosornis*, *Chlorospingus*, *Diglossa*; García-Moreno unpubl.), *Lepidocolaptes* woodcreepers (García-Moreno & Silva 1997), and *Ochthoeca* chat-tyrants (García-Moreno et al. 1998). Opportunistic sampling was supplemented by specific efforts to fill in collecting gaps and to make comparisons across a potential dispersal barrier. We also used published molecular data for other Andean groups. While ca. 100 species were covered altogether, the sampling was insufficient for describing population structures within species.

To estimate evolutionary time we used genetic distances (uncorrected), as well as Kimura's two parameters, and assumed three different rates of nucleotide substitutions: 2% per million years (Klicka & Zink 1997, and references therein), 10% 3rd position substitutions per million years, and 0.5% 3rd position transversions per million years (Irwin et al. 1991). The two latter measures complement each other: The total 3rd position rate is ideal for comparing closely related taxa, but is poor when comparing distantly related ones, because of saturation; the 3rd position transversion rate tracks the relative age of branches over a long evolutionary time frame (Burns 1997) but provides few data for comparing closely related taxa where there are few (or no) transversions.

We compared divergence data for taxa occurring in allopatry, parapatry, and sympatry. To minimize effects due to the possibility of different substitution rates in different groups we restricted these comparisons to those within genera and groups of related genera. We assume that the substitution patterns within such groups reflect the chronology of events rather than variation in substitution rates. Even in comparisons between groups, there is little reason to fear dramatic differences in substitution rates, since all groups (except the hummingbirds) are passerine birds of fairly constant size and generation time characteristics. A large portion of them even belong in one close-knit group of 'nine-primaried oscines'.

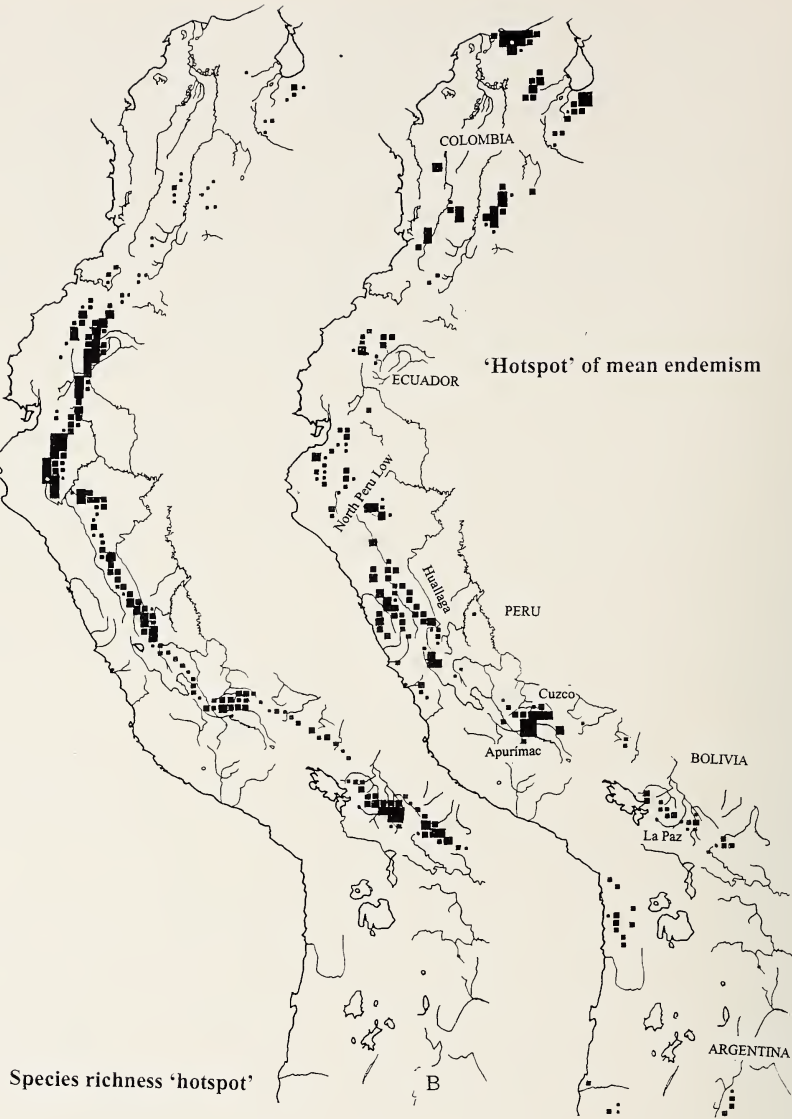


Fig.1: 'Hotspots' of species richness and mean endemism for highland birds in the tropical Andes region. 'Hotspots' are defined here as the 200 top-scoring cells: the first 50 cells have the largest symbols, etc. The mapping was done using the WorldMap software (Williams 1994) in the form of conservative range maps (in a 15'x15' grid) for all bird species which are well established above 2500 m (at least locally) (see Fjelds  et al. 1999). The mean endemism is calculated as the mean inverse range-size for all species. These maps were made from a datafile constructed using a phylogenetic species concept (see Fjelds  in press for details); however, with the 15' resolution, the species richness is virtually unaffected by the species concept used.

Results

Biogeographic patterns

The regional patterns of species richness and endemism for high Andean birds are illustrated in fig.1. The species richness 'hotspot' (fig.1A) follows the band of humid montane forest fringing the upper Amazon Basin. Despite some local variation, there is no general latitudinal trend within this range (Fjelds  et al. 1999). Congeneric species often replace each other in different elevational zones (long parallel distributions in fig.2) or they replace each other sharply along the Andes, sometimes across physical barriers, such as the North Peru Low, but sometimes in places with no conspicuous barrier (fig.2).

The endemism is locally aggregated (fig.1B). Some aggregates extend right across a habitat gap, as range-restricted birds may inhabit cloudforest fragments on either side of a deep (dry) valley, many of which interrupt the eastern Andean cloud-forest band (Fjelds  1995).

Case studies (starting with groups which radiated mainly before the Pleistocene) *Ochthoeca* chat-tyrants. These are common birds of Andean shrubby vegetation, most species being widespread along the length of the Andes, with broadly overlapping ranges (fig.2) but some habitat segregation (Garc a-Moreno et al. 1998). On the basis of the level of genetic divergence, and a few sharp replacements along the Andes, some of the traditionally accepted species may represent pairs of sister species (*cinnaomoeiventris/thoracica* and *frontalis/spodionota*). All species which are distributed along long sections of the Andes show some local variation, e.g., in the expression of wingbars. Apart from this subspecific differentiation, the radiation predates the upper Pleistocene (figs.2 and 3, Garc a-Moreno et al. 1998). Because of the extensive sympatry, the biogeographic signals are often lost. However, an adaptive shift is apparent from bushy highland habitat in the deep branches to closed montane forest, and bamboo areas in the lower montane zone in the top branch.

Scytalopus tapaculos (Arctander & Fjelds  1994, and some unpublished data). This is a very complex group of secretive, sooty-grey birds which scurry like mice through dense understory of humid montane forest. A large number of species (which are most safely identified by songs and calls) replace each other sharply in different elevational zones, or in different mountain ranges. As most species are poorly known or only recently recognized (Krabbe & Schulenberg 1997) the sampling was incomplete (and the group is therefore not shown in figs.2 and 3). However, a 10-15% sequence divergence in most comparisons suggests that the population subdivision is ancient. In all comparisons of species which replace each other elevationally on a slope, it was found that each was most closely related to a taxon inhabiting another mountain range (four-taxon tests). This strongly supports the view that the speciation was allopatric and that sympatry (with sharp elevational segregation) is secondary.

Tanagers, Thraupinae. This large group showed a strong radiation during the Miocene (Sibley & Ahlquist 1990, Burns 1997). We studied variation in the genus

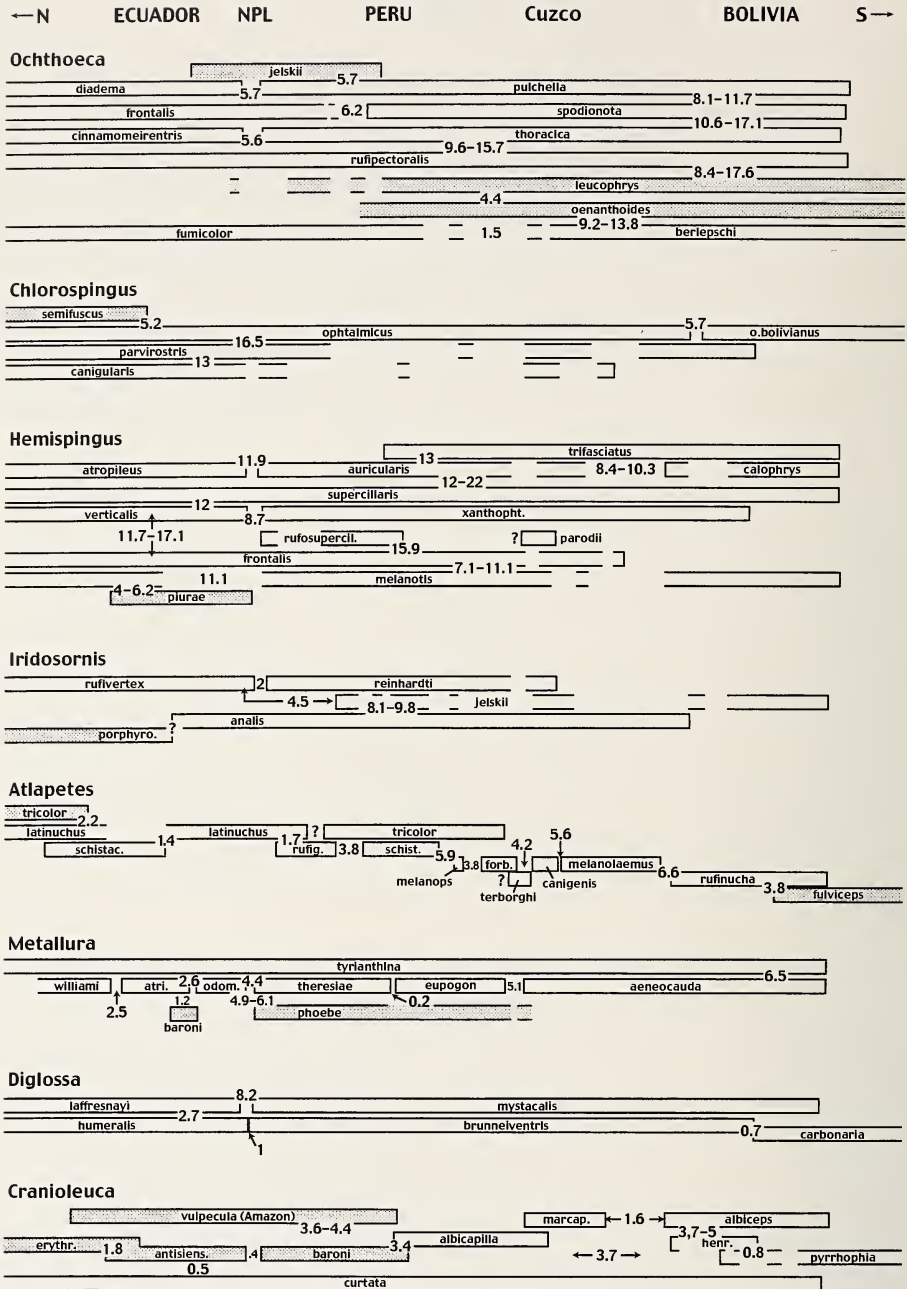


Fig. 2. Spatial replacements of taxa along the cis-Andean slope of Ecuador, Peru and Bolivia (with taxa inhabiting adjacent intermontane and trans-Andean areas shaded). Figures mark the sequence divergence between closely related groups which inhabit adjacent slopes or different altitudinal zones on the same slopes.

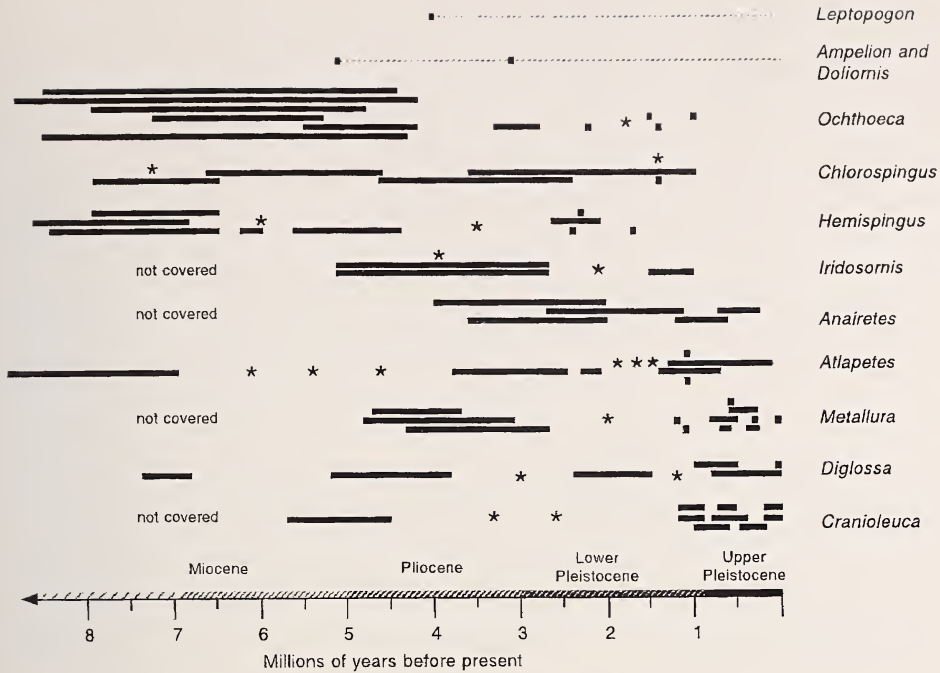


Fig. 3. Estimated ages for phylogenetic branches in ten groups of Andean birds. Some of these groups began to diversify before the upper Miocene, but because of the incomplete sampling we will not estimate their time of origin. The bars mark the maximum and minimum estimates of the timing, according to three methods specified in the text, of a specific phylogenetic node. The margins of uncertainty are large for early events, but much smaller for the most recent events. An * indicates that a species was lacking in our sampling, and this information is placed according to our judgement of where the species should be in the phylogeny.

Chlorospingus, which belongs in a rather deep branch, and three more recently radiating groups (*Hemispingus*, mountain tanagers (mainly *Iridosornis*), and flowerpiercers *Diglossa*).

Hemispingus shows similar distribution patterns to *Ochthoeca*, with many widespread but elevationally segregated species, but also some replacements (fig.2). Three main clades form a trichotomy that we date to the upper Miocene: (1) a clade with long branches and short internodes comprising eyebrowed birds (tree topology *trifasciatus* [*atropileus* {*auricularis*, *calophrys*}]); (2) mostly grey birds (*superciliaris* [*xanthophthalmus*, *verticalis*]); (3) mostly ochraceous birds (*rufosuperciliaris* [*piurae* {*frontalis*, *melanotis*}]). The differentiation may precede the Pleistocene, even among sister species like *verticalis* and *xanthophthalmus* (fig.3). Two *M. melanotis* representing two subspecies have identical DNA sequences but show an early (Pliocene) divergence from the Tumbesian 'subspecies' *piurae* (which may be a valid species).

For *Chlorospingus* our sampling was incomplete, but among the Andean species we found *canigularis* to be basal, *flavigularis* and *parvirostris* being sister species,

and the widespread and polytypic *opthalmicus* being closest to *semifuscus* of the wet northern Pacific slope. Interestingly, the Bolivian population of *opthalmicus*, which superficially resembles birds from Colombia and Venezuela rather than adjacent Peruvian birds, may be a distinctive species (diverging since the mid-Pleistocene). The radiation predates the upper Pleistocene (fig.3).

Iridosornis, a group of colourful mountain tanagers, shows vicariance as well as elevational segregation (fig.2). The tree topology is still ambiguous. Most speciation events were in the Pliocene, but the two parapatric sister species *rufivertex* and *reinhardtii* may have diverged in the upper mid-Pleistocene.

We studied the *Diglossa carbonaria* group and samples of *D. laffresnayii* and *mystacalis*, using *D. sittoides* as an outgroup (see Hackett 1995). The *mystacalis-laffresnayii* complex may be paraphyletic, diverging in the Pliocene. The *D. carbonaria* complex is widely distributed in bushy habitats throughout the tropical Andes region, with sharp geographical displacements (fig.2) of birds with strikingly different pigment saturations. There is very little genetic variation in this branch (figs.2 and 3) from Colombia to Bolivia despite the sharp replacements, and there is limited hybridization only in one of the contact zones (Graves 1982).

We also have data for a few *Basileuterus* wood warblers (unpublished), which may be very close to the tanagers (Sibley & Ahlquist 1990, Burns 1997). This group is incompletely sampled but our results suggest speciation events of a similar age as in tanagers (tab.1).

Metallura hummingbirds. García-Moreno et al. (1999a) evaluated the idea of Graves (1988) that the differentiation is strongest at the treeline since the narrow physical configuration of this habitat implies high risks of local elimination and isolation of relict populations. We compared the relationship between two assumed (and verified) sister taxa: *M. tyrianthina*, ubiquitous in the humid montane zone of the tropical Andes region, and the *M. aeneocauda* group, which is narrowly bound to humid treeline shrubbery. Diversification proceeded through the Pliocene and Pleistocene, with one very recent speciation event (*M. eupogon/theresia*, fig.3). We confirmed that the clade of treeline forms was deeply differentiated, starting with an early isolation of the southernmost population (*aeneocauda*) and range fragmentation progressing northwards. An aberrant species in mist vegetation above the Peruvian coastal desert (*M. phoebe*, large and melanistic) is closest to its geographically nearest neighbours in southern Ecuador and may owe its aberrant morphology to strong directional selection in its special environment. Otherwise, the treeline clade is characterized by checkerboard variation in phenotypic characters (Graves 1980), while in *M. tyrianthina* there is a more consistent latitudinal trend with the most derived phenotypes in the north (Heindl & Schuchmann 1998).

Atlapetes brush-finches (García-Moreno & Fjeldså 1999). Phenotypically distinct forms replace each other sharply, at different altitudes, on adjacent humid and rain-shadowed slopes, along the Andean slope, or in some cases in a mosaic (fig.2, Remsen & Graves 1995a,b). In the traditional classification (Paynter 1970), grey and yellow-and-green species are placed in different groups, with many similarly

coloured populations ranked as subspecies. The DNA data did not support this subdivision (García-Moreno & Fjeldså 1999a). With the reservation that northern and west-slope populations were not included in our study, three main branches were demonstrated, diverging at the Plio-Pleistocene transition, each comprising geographically adjacent but morphologically different forms, and with most speciation events in the mid-Pleistocene (figs.2 and 3). Plumage colours did not faithfully reflect the evolutionary trajectories in this genus, as adjacent and related populations may be strikingly differently pigmented. The data also show that many forms, currently ranked as subspecies, are genetically more divergent than some *Atlapetes* species which are sympatric (although segregated in adjacent elevational zones). Since the replacements are abrupt, sometimes in places with no habitat discontinuities, and with scarcely any signs of hybridization, we will consider these forms as valid and competing species.

Table 1: Sequence divergence (uncorrected) between related species which are sympatric (syntopic or segregated in adjacent elevational zones along the Andean slopes) and parapatric (replacing each other in adjacent territories along the Andes, with or without a separating physical barrier) (Mann-Whitney U-test).

genus		n	mean distance (range)	probability	significance level
<i>Scytalopus</i>	sympatric	19	0.161 (0.084-0.168)	p=0.010	**
	parapatric	6	0.098 (0.063-0.119)		
<i>Ochthoeca</i>	sympatric	20	0.118 (0.044-0.157)	p=0.011	**
	parapatric	8	0.079 (0.056-0.143) ¹		
<i>Hemispingus</i>	sympatric	27	0.143 (0.071-0.222)	p=0.014	*
	parapatric	3	0.103 (0.087-0.119)		
<i>Chlorospingus</i>	sympatric	7	0.122 (0.087-0.165)	p=0.058	+
	parapatric	4	0.066 (0.025-0.130)		
<i>Iridosornis</i>	sympatric	4	0.080 (0.053-0.098)	p=0.157	n.s.
	parapatric	1	0.020		
<i>Diglossa</i>	sympatric	8	0.107 (0.027-0.134)	p=0.025	*
	parapatric	3	0.033 (0.007-0.082)		
<i>Metallura</i>	sympatric	7	0.072 (0.064-0.080)	p=0.015	*
	parapatric	8	0.037 (0.002-0.086)		
<i>Atlapetes</i>	sympatric	8	0.128 (0.042-0.143) ²	p=0.001	***
	parapatric	9	0.040 (0.014-0.066)		
<i>Cranioleuca</i>	sympatric	3	0.044 (0.042-0.045)	p=0.010	**
	parapatric	11	0.019 (0.005-0.041)		
<i>Anairetes</i>	sympatric	8	0.044 (0.054-0.079)	p=0.123	n.s.
	parapatric	1	0.013		
<i>Basileuterus</i>	sympatric	3	0.083 (0.070-0.105)	p=0.180	n.s.
	parapatric	1	0.033		

¹) Comparisons include *Tumbezia salvini*

²) Comparisons include *Buarremon brunneinucha*

Cranioleuca (García-Moreno et al. 1999b) belongs in the complex 'spinetail' group, which radiated mainly along the eastern Brazilian-Andean track. We focused on what seemed to be a natural group of species which replace each other along this track, mainly in woodland and thornscrub habitats, and with a distinctive checkerboard variation of phenotypes (Maijer & Fjeldså 1997). The DNA data suggested a recent and rapid radiation (mainly in the upper Pleistocene, fig.3) with somewhat deeper splits between the main clades, both of which include species which inhabit other ecological zones and which diverge phenotypically from the focal group. This suggests that in addition to a random sorting of phenotypic traits in the focal group there were several adaptive shifts into humid forest or even lowland forest (swamp-forest and species-poor islands of whitewater rivers). The radiation is not fully resolved and within the most closely knit species groups geographically unstructured haplotypes were demonstrated, suggesting retained ancestral polymorphism and random lineage sorting (Avice 1994).

Other groups

Ampelionid cotingas (Arctander & Fjeldså manuscript; fig.3) show deep branches indicating a mid-Miocene differentiation of plantcutters (*Phytotoma*, in dry *Prosopis* woodlands) and the humid forest lineages *Ampelion* (*A. rubrocristatus*, which is ubiquitous in the montane forests of the tropical Andes region, and *A. rufaxilla*, which is more local in high-rainfall areas), *Doliornis* (very local in elfin forests along the eastern Andean ridge) and *Zaratornis* (endemic to *Polylepis* and cloud forests above the central Peruvian coastal desert and in the adjacent Cordilleras Blanca area). *Doliornis* shows a mid-Pleistocene vicariance (*D. remseni* in the northern central Andes of Colombia and locally in Ecuador; *D. sclateri* in central Peru).

Flycatchers of the genus *Leptopogon* are represented by four species, *amaurocephalus* being widespread in the tropical lowlands, *superciliaris* in the submontane zone of the Andes, and *taczanowskii* and *rufipectus* in the lower montane forest north and south of the North Peru Low. MtDNA data (Bates & Zink 1994) show the topology (*amaurocephalus* [*superciliaris* {*taczanowskii*/*rufipectus*}]), with the most recent split at 4 Mya (fig.2).

Lepidocolaptes woodcreepers (García-Moreno & Silva 1997) are widespread in Neotropical forests and savanna woodlands. The mtDNA data suggest that the split between the species of forest and savanna woodland took place as recently as 2 Mya, and the separation of *L. lacrymiger*, which is distributed in montane forest along the entire tropical Andes region, is a similar recent event.

Adelomyia melanogenys. The distribution of haplotypes among ten individuals from different sites in Ecuador, Peru and Bolivia (García-Moreno unpubl.) showed a single (poorly resolved) cluster of haplotypes, except for the single Bolivian taxon (the distinctive subspecies *inornata*) which may have diverged in the Pliocene. The latter could represent a distinctive species, although Zimmer (1951) claims evidence of hybridization in Cuzco.

Tit-tyrants (*Anairetes*, *Uromyias*), widespread birds of bushy Andean habitats, diversified mainly around the Plio-Pleistocene transition with one vicariance event in the upper Pleistocene (fig.3, Roy et al. 1999). Andean pipits (*Anthus*), which are

widespread grassland birds with considerable range overlaps between species, speciated in the lower to mid-Pleistocene (Volker 1999). *Asthenes* spinetails, inhabiting the same ecological zone, show as slight genetic differences as *Cranioleuca* (Arctander 1991 and unpublished). American *Carduelis* species, which are widespread in bushy habitats, with large range overlaps, radiated within the last 3 Mio years (Arnaiz-Villena et al. 1998). A molecular study of conebills (*Conirostrum*), which are also widespread in bushy and wooded habitats, suggests that this group radiated in the Andes in the early Pleistocene, and that it is paraphyletic with respect to *Oreomanes fraseri*, a highly specialized bird of the high-elevation *Polylepis* woodlands (Nielsen & Arctander submitted). The divergence is estimated at 2.9 Mya, which matches well with the abundance of *Polylepis* pollen since 3.1 Mya.

Chronogram

Fig.3 shows the temporal distribution of phylogenetic node since the upper Miocene. It should be noted that each node is represented by a bar which shows the range of different time estimates, which is considerable for the Mio- and Pliocene events but much smaller for those in the upper Pleistocene. Assuming that all groups have similar substitution rates, that calibrations estimated for mammals (Irwin et al. 1991) apply, and that our species sampling is representative, we find that the diversification of Andean birds was well spaced throughout the time period, except maybe for more intensive speciation in the upper Miocene, Pliocene and mid-Pleistocene. It should be noted that the tanager genera in fig.3 show very different chronograms, although they are closely related (Burns 1997) and inhabit similar ecological zones.

A few cases in *Diglossa* and *Cranioleuca* suggest that speciation may sometimes take place within a time frame of one or two glacial periods (see Graves 1982 and Majer & Fjeldså 1997 regarding species rank). However, this happened only in few lineages, and never as a series of events which might correspond to successions of glacial periods. Other lineages showed no speciation in the upper Pleistocene, and this even applies to species inhabiting ecoregions which were extensively glaciated (e.g., *Anairetes alpinus*, *Ochthoeca fumicolor* and *oenanthoides*, *Oreomanes fraseri*). Speciation events within the period of marked Pleistocene glaciations are: *Metallura williami/atrigularis/baroni* and *M. theresiae/eupogon*, *Cranioleuca antisimensis/baroni/curtata* and *erythrops*, *Cranioleuca marcapatae/albiceps* and *C. obsoleta/pyrrhophia* and *henricae*, *Diglossa humeralis/brunneiventris/carbonaria*. In *Atlapetes*, some speciation events may correspond to the early part of the period.

Parapatric and sympatric species

We compared the divergence data for taxa occurring in allopatry, parapatry, and sympatry. Sympatry refers to co-existence on the same slope, although sometimes with elevational segregation. The allopatric species represent a 'mixed bag', ranging from closely related species isolated in different mountains to remotely related species which inhabit different parts of the Andes and sometimes different life zones (fig.2). The number of comparisons are insufficient for testing for

differences between sister species which are local/patchy and not strictly parapatric, those which are widespread and common up to a habitat discontinuity which separates them, and those which are in actual parapatric contact. We therefore present a statistical comparison of para- and sympatric species only (tab.1).

For every taxonomic group, the sympatric species were all strongly divergent compared with most parapatric species. In all cases, except for *Anairetes*, *Basileuterus* and *Iridosornis* (where we had only a single parapatric comparison), we found a significant difference in the genetic divergence exhibited by sympatric and parapatric species (tab.1), even though some species that replace each other in adjacent mountains (i.e., parapatric in our terminology) are genetically distinct. Also taking into account the results by Arctander & Fjelds  (1994) (and Patton & Smith 1992 for Andean mice), we reject the view that speciation can proceed through differential selection across an ecological gradient (Endler 1982). Speciation starts with isolation on different slopes, and sympatry (with elevational and other kinds of segregation) becomes possible only after a considerable time lag.

The relative role of the North Peru Low

The North Peru Low (NPL, see fig.1) is a geologically complex zone with a relatively low and tectonically splintered western cordillera, and an erosion gap through the eastern Andean ridge probably predating the uplift of this cordillera (R s nen et al. 1987). This gap has been regarded as a main barrier causing speciation of highland birds (Vuilleumier 1969, Graves 1985, O'Neill 1992, Stotz et al. 1996).

The species replacements across the gap represent a wide range of time scales, from 0.4 to 11.9% sequence divergence ($5.7 \pm 4.06\%$, $N=12$). This can be compared with the variation across the NPL within species, which varied from 0.3 to 6.1 (in *Adelomyia melanogenys*) ($2.8 \pm 1.81\%$, $N=9$; or 0.3, 0.7, 2.4, 4.1 and 6.1 % for five pairwise comparisons of samples collected within 150 km of the gap).

The species replacements, and the intraspecific comparisons, demonstrate isolation and dispersal at many time scales. The sister species separated by the NPL included in our study inhabit mainly upper montane forest. Parker et al. (1985) suggested that major rivers such as the Mara  n may not affect the dispersal of mid-elevation forest birds so much. However, a considerable divergence was found in the mid-elevation genera *Adelomyia* and *Leptopogon*. Several northern taxa are established (without conspicuous morphological differentiation) immediately south of the NPL, on the eastern ridge, displacing a southern (sister?) taxon slightly to the south, where there is no conspicuous barrier (Fjelds  & Krabbe 1990). Very few cases exist of a displacement slightly north of the NPL.

For several groups we found that the principal split was not at the NPL but in the southern part of the tropical Andes region (in the *Metallura aeneocauda* group with 5.1-8.5% sequence divergence, *Atlapetes* with 4.9-8.0%, *Cranioleuca* with 2.7-4.0%, *Hemispingus* (eye-browed group) with 8.4-10.3%) (Stotz et al. 1996). This split separates populations in a southern area which includes the Apur mac-Cuzco and La Paz centres of endemism (fig.1). Within currently recognized species, deep

southern splits were documented in *Adelomyia melanogenys* (7.7-10.1%) and *Chlorospingus ophthalmicus* (5.7%). A dozen montane forest birds, which are widely distributed near the equator, may have an isolated population south of Cuzco or in the Bolivian yungas (Fjeldså & Krabbe 1990).

The endemics of the dry forests and local cloudforests of the Tumbes region (southwestern Ecuador and northwestern Peru) also vary in age, which may be related to the predictable mist front (and therefore persistence of mist vegetation) in this region, in addition to the isolating effect of the Andes (Best & Kessler 1995, Fjeldså 1995, García-Moreno et al. 1998).

Discussion

In the past, many authors related the speciation patterns in the Andes to topographic barriers. We accept that the uplift of the northern Andes must have provided numerous opportunities for speciation by orographic isolation. However, it is important to note that barriers which separate sister species today were not necessarily the initial cause of speciation (Cracraft & Prum 1988, Louette 1992). Only a detailed study of historical population structures can reveal whether populations inhabiting different slopes diverged because of the barrier between them, or whether the replacements are secondary contact zones.

Speciation events have also been related to specific Pleistocene glaciations (Traylor 1985, Fjeldså 1992, Heindl & Schuchmann 1998). This may offer plausible scenarios. However, direct evidence of the timing is lacking and it is difficult to provide robust tests of effects of climatic cycles with no beginning or end phase.

We tried to evaluate the traditional interpretations using the molecular clock concept, assuming that it is better to have a crude clock than no clock at all (Bromham et al. 1999). We will stress that reliable calibrations of evolutionary rates are difficult to make, especially as the fossil record is very fragmentary. Various statistical tests of the relative uniformity of base substitutions along different lineages have been performed (see Mindell & Thacker 1996, Avise & Walker 1998, Bleiweiss 1998 a, Waddell et al. 1999). Bleiweiss (1998 a,b) found that hummingbirds show a high rate of mtDNA divergence, but with a markedly reduced rate in highland hummers. The different rate tests suggest fairly uniform accumulation of base substitution within restricted taxonomic groups (such as nine-primaried oscines, comprising tanagers and *Atlapetes* in our study; Burns 1997). Many authors come to a similar 2% estimate using very different groups of birds (note 11 in Klicka & Zink 1997). Because of the uncertainty we used several different estimates. This does not help with the uncertainty caused by the relatively short sequences we used, although because of the good taxon sampling we are confident about the phylogenetic results (see e.g., Graybeal 1998). Our time estimates should be taken as a rough measure and should not be overinterpreted.

We could not support a synchrony of speciation events across taxonomic groups (and particularly not among the closely related 'nine-primaried oscines', where each genus shows its own pattern in fig.3). In our data set there are no indications of successive speciations during the sequence of eight large-scale climatic cycles in

the upper Pleistocene (Hooghiemstra et al. 1993), as is sometimes implied in the literature. It is important to note that several groups showed no speciation in the upper Pleistocene, while others showed several speciation events near the mid- to upper Pleistocene boundary. Some of these (e.g., *Atlapietes*) could represent the simultaneous break-up of several lineages, in which case attempts to resolve them would be futile (Stepien & Kocher 1997).

We have to take into account that the density of nodes in the most recent past is accentuated by our sampling regime, and also potentially by the extinction of deeper lineages. A high level of phylogenetic resolution suggests slow rates of historical isolation compared with the coalescence time, except in the *Diglossa carbonaria* group and *Cranioleuca*.

We therefore conclude that the diversification of the Andean avifauna proceeded throughout the period of uplift and gradual formation of new habitats in the northern Andes since the Miocene (Wijninga 1995, Hooghiemstra & van der Hammen 1998). Similarly, Bleiweiss (1998 c) related the rapid radiation of hummingbirds since the lower Miocene to the creation of new habitats by major geological and climatic upheavals and multiple dispersals.

Even though the usefulness of the molecular clock is debatable, we prefer to accept this kind of evidence rather than perpetuating a model which is based on belief more than data. Our interpretation of those groups which show a marked vicariance pattern of mid-Pleistocene age is that this pattern could often persist despite the dramatic ecoclimatic changes in the upper Pleistocene. The idea of speciation pulses driven by glacial-interglacial cycles appears to be a failed paradigm (Klicka & Zink 1997) (although this does not exclude population structuring or some speciation events related to glacial isolation).

The typical mode of speciation must be allopatric or parapatric, by isolation in different (but usually adjacent) montane areas (as also suggested by Patton & Smith 1992 for Andean rodents, and by Arctander & Fjeldså 1994). In the groups we studied, species with small distributions are found mainly in recently differentiated clades (fig.2). We infer from this (and from tab.1) that sympatry comes later, after long isolation, adaptive change and dispersal. A rapid dispersal can in some cases be supported by low levels of morphological and genetic differentiation along the Andes (with examples showing even zero divergence over 1000 km). In many lineages, the biogeographic signals lie buried in multiple cycles of redistribution, and detailed studies of historical population structures would be needed to retrieve them. We could also use our current data under the assumption that rates of base substitution will be modest in populations which remain *in situ* compared with those which colonize new areas, with founder effects and shifting selection pressures. Using outgroup comparisons, we found that the *Ochthoeca* radiation involved southern origins, followed by northwards dispersal for *O. fumicolor*, *leucophrys/oenanthoides*, *pulchella* and *spodionota*. However, no such polarity could be established in *Metallura*, and for other taxa with long linear distributions, where our sampling was inadequate.

The random phenotypic variation in lineages with species replacements along the Andes (Graves 1982, 1985, Remsen 1984 a,b, Remsen & Graves 1995 a,b, Maijer & Fjeldså 1997, García-Moreno & Fjeldså 1999) suggest that speciation starts with

divergence of tiny isolates. This is also indicated by the random sorting of haplotypes in *Cranioleuca* populations inhabiting relictual forest patches (García-Moreno et al. 1999b). Morphological characters would fail to retrieve the branching patterns that were substantiated by the molecular markers. Subtle differences between small isolated populations in relict woodlands within the highlands may also reflect random processes in small populations but may not be conducive to speciation (Vuilleumier 1984 b).

Our data provide strong indications that geographic replacements can sometimes be maintained over long time spans (e.g., *Atlapetes*). The reason could be a lack of directional selection where populations remain in the same area. In this situation we expect populations to diverge only by neutral drift.

It can also be inferred that parapatric taxa are valid species: they represent cohesive and genealogically concordant lineages of individuals that share a common fertilization system through time and space, represent independent evolutionary trajectories, and demonstrate essential but not necessarily complete reproductive isolation from other such units (Johnson et al. 1999). Naturally, replacements between such incompatible species are most easily maintained where there is a physical barrier, although a few replacements do exist on slopes with no obvious barrier.

Overall, our results are consistent with our initial predictions based on the model of divergence of relict populations (p.26). Within the Andes, certain areas may be inherently stable because of local high pressure areas, topographic conditions which cause stable (laminar) mist formation on certain slopes, or specific projecting mountain ridges moderating the impact of cold south polar winds. The most conspicuous of such areas are just north of the Tunari highlands (Cochabamba, Bolivia), where the projecting Cordilleras Mosetenes and Cocapata form a marked shelter against the impact of cold southern winds, causing a benign and stable climate in the Cotacajes drainage and in the southern Yungas of La Paz. A similar area exists in Cuzco and Apurímac in Peru, where a fan of mountain ridges provides a similar shelter. The south polar winds today cause short but frequent spells of cold winter weather in the lowlands and Andean slopes in the southern part of the tropical zone. Servant et al. (1993) suggest that the vegetational changes in tropical South America during the Pleistocene were driven mainly by the increased impact of these winds; however, they are potentially disturbing also on other time scales.

Species respond individually when tracking the environmental oscillations within their geographical ranges (Walter & Paterson 1993, Colinvaux et al. 1996). The high levels of environmental disturbance (even within fairly continuous habitat) imply high levels of faunal turnover sorting out some of the rarer species from local communities (Hubbell 1999). The best prospects for persistence of relict populations are therefore in places with slight local faunal turnover. According to this interpretation, speciation may proceed without barriers which would isolate entire communities. Instead diversification is a random process where only some species undergo relictuation and independent evolution of each isolate. Speciation relates in this case to the intrinsic properties of specific places rather than to the barriers between them.

Hooghiemstra & van der Hammen (1998) suggest that because of the concave arrangement of the cis-Andean slope, this region would have been continuously forested during the Pleistocene. According to the mechanism outlined above, some species ranges could nevertheless be fragmented at any time, and the isolation of populations would last a long time because of the high general levels of climatic change and faunal turnover.

It is conceivable that many relict populations do go extinct. However, repeated bottleneck effects may also remove deleterious alleles which could give inbreeding problems (Templeton & Reed 1984, part III in Loeschcke et al. 1994). Possibly, some small isolates are exposed to novel selective regimes in unique environments to adapt to new conditions (as indicated by size variations in *Cranioleuca* [Maijer & Fjeldså 1997] and by rapid phenotypic changes in *Oreomanes* and *Metallura phoebe*) and this opens new avenues for speciation (Walter & Paterson 1994).

Perspectives

We now need to ask ourselves whether relict populations are isolates which persist for some time but eventually vanish - or whether they represent a potential source of recruitment to the regional species pool? We have already suggested that dispersal takes place. Over the geological period considered, even a low rate of successful expansions could substantially contribute to the regional species pool. However, dispersal and species pump models are extremely difficult to evaluate. We need to study

(1) community structure (as high local turnover means that range-restricted species will be rare, while low turnover allows them to become locally abundant; Hubbell 1999) and

(2) molecular data to document the historical community structure using large samples from many localities, rapidly evolving sequences (e.g., control region, nuclear microsatellites) and statistics based on coalescence theory (Hudson 1990, Hartl & Clark 1997).

Many field studies (Fjeldså & Kessler 1996, Andersen et al. 1999) indicate that viable populations of Andean birds can persist in tiny fragments of natural habitat in severely degraded highland landscapes. This gives some hope for conservation, but the aggregated pattern of endemism (fig. 1b) nevertheless means that in order to minimize extinction we need to define clear priorities. The key problem for conservation of Andean highland birds is that peak concentrations of endemics are often immediately adjacent to densely populated areas (Fjeldså & Rahbek 1999, Fjeldså et al. 1999). Possibly, the ecoclimatic conditions moulding the pattern of endemism also provided predictable conditions for agriculture in the highlands. This means that the main challenge today for preventing extinction in this region will be to maintain patches of natural habitats, and biodiversity, within areas that are populated. The key problem will be to support other landuse methods, raising the production in some areas and stopping the intensive use of fire on all high ridges to maintain extensive grazing (Fjeldså & Kessler 1996).

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References

- Andersen, B.G. & H.W. Borns (1994): The ice age world. – Scand. Univ. Press, Oslo.
- Andersen, P.N., T. Hjärsen & N.M. Williams (1999): Monitoring and management of high Andean biodiversity – a study from Cochabamba, Bolivia.- DIVA Tech. Rep. 6. National Environmental Research Institute, Kalø, Denmark.
- Arctander, P. (1991): Avian systematics by sequence analysis of mtDNA. – Acta XX Congr. Int. Orn.: 619-628.
- Arctander, P. & J. Fjeldsø (1994): Andean tapaculos of the genus *Scytalopus* (Aves, Rhinocryptidae): a study of speciation using DNA sequences. – pp. 205-225 in: Conservation Genetics (eds Loeschcke, V., J. Tomiuk & S.K. Jain).- Birkhäuser, Basel.
- Arctander, P. & J. Fjeldsø (manuscript): The relationships of plantcutters, (Phytotoma, Aves), re-analyzed using DNA sequence data. – Steenstrupia.
- Arnaiz-Villena, A., M. Alvarez-Tejado, V. Ruíz-del-Valle, C. Garcia-de-la-Torre, P. Varela, M.J. Recio, S. Ferre & J. Martínez-Laso (1998): Phylogeny and rapid northern and southern hemisphere speciation of goldfinches during the Miocene and Pliocene epochs. – Cell. Mol. Life Sci. 54: 1031-1041.
- Avise, J.C. (1994): Molecular markers, natural history and evolution. – Chapman & Hall, New York.
- Avise, J.C. & D. Walker (1998): Pleistocene phylogeographic effects on avian populations and the speciation process. – Proc. R. Soc. Lond. B. 265: 457-463.
- Bates, J.M. & R.M. Zink (1994): Evolution into the Andes: molecular evidence for species relationships in the genus *Leptopogon*. – Auk 111: 507-515.
- Best, B.J. & M. Kessler (1995): Biodiversity and conservation of Tumbesian Ecuador and Peru. – BirdLife, Cambridge, U.K.
- Bleiweiss, R. (1998 a): Relative-rate tests and biological causes of molecular evolution in hummingbirds. – Mol. Biol. Evol. 15: 481-91.
- Bleiweiss, R. (1998 b): Slow rate of molecular evolution in high-elevation hummingbirds. – Proc. Natl. Acad. Sci. USA 95: 612-616.
- Bleiweiss, R. (1998 c): Origins of hummingbird faunas. – Biol. J. Linn. Soc. 65: 77-97.
- Bromham, L., M.J. Phillips & D. Penny (1999): Growing up with dinosaurs: molecular data and the mammalian radiation. – Trends Ecol. Evol. 14: 113-118.
- Burns, K.J. (1997): Molecular systematics of tanagers (Thraupinae): evolution and biogeography of a diverse radiation of Neotropical birds. – Mol. Phyl. Evol.

72: 334-348.

- Carson, H.L. (1990): Increased genetic variance after a population bottleneck. – *Trend Ecol. Evol.* 5: 228-230.
- Colinvaux, P.A., P.E. de Oliveira, J.E. Moreno, M.C. Miller, & M.B. Busch (1996): A long pollen record from lowland Amazonia: forest and cooling in glacial times. – *Science* 274: 85-88.
- Cracraft, J. & R.O. Prum (1988): Patterns and processes of diversification: speciation and historical congruence in some Neotropical birds. – *Evolution* 42: 603-620.
- Endler, J.A. (1982): Pleistocene forest refuges: Fact or fancy?. – pp. 641-657 in: *Biological diversification in the tropics* (ed. Prance, G.T.). – Columbia Univ. Press, New York.
- Fjeldså, J. (1992): Biogeographic patterns and evolution of the avifauna of relict high-altitude woodlands of the Andes. – *Steenstrupia* 18: 9-62.
- Fjeldså, J. (1994): Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. – *Biodiver. Conserv.* 3: 207-226.
- Fjeldså, J. (1995): Geographical patterns of neoendemic and older relict species of Andean birds: the significance of ecological stability areas. – pp. 89-102 in: *Biodiversity and conservation of Neotropical montane forests* (eds Churchill, S.P., H. Balslev, E. Forero & J.L. Luteyn). – The New York Botanical Garden.
- Fjeldså, J. (in press): Choosing priority areas for global conservation: the relevance of systematics. – *Envir. Conserv.*
- Fjeldså, J. & N. Krabbe (1990): *Birds of the High Andes*. – Apollo Books, Svendborg, and the Zoological Museum, Copenhagen.
- Fjeldså, J. & M. Kessler (1996): Conserving the biological diversity of *Polylepis* woodlands of the highland of Peru and Bolivia. A contribution to sustainable natural resource management in the Andes. – Nordeco and Zoological Museum, Copenhagen.
- Fjeldså, J., E. Lambin & B. Mertens (1999): Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. – *Ecography* 22: 63-78.
- Fjeldså, J. & C. Rahbek (1999) Continent-wide diversification processes and conservation priorities. – pp. 139-160 in: *Conservation in a changing world* (eds Mace, G.M., A. Balmford & J.R. Ginsberg). – Cambridge U.P., Cambridge, U.K.
- Fjeldså, J., M.K. Bayes, M.W. Bruford & M.S. Roy (in press): Biogeography and diversification of African forest faunas: implications for conservation. – In: *Rainforests – past and future* (ed. Moritz, C.). – Chicago U.P., Chicago.
- Flenley, J. (in press): Palyno-diversity and the super rainforest. – In: *Rainforests – past and future* (ed. Moritz, C.). – Chicago U.P., Chicago.
- García-Moreno, J., P. Arctander & J. Fjeldså (1998): Pre-Pleistocene differentiation among chat-tyrants. – *Condor* 100: 629-640.
- García-Moreno, J., P. Arctander & J. Fjeldså (1999a): Strong diversification at the treeline among *Metallura* hummingbirds. – *Auk* 6: 702-711.

- García-Moreno, J., P. Arctander & J. Fjeldså (1999b): A case of rapid diversification in the Neotropics: Phylogenetic relationships of *Cranioleuca* spinetails (Aves, Furnariidae). – *Molec. Phyl. Evol.* 12:273-281.
- García-Moreno, J. & J. Fjeldså (1999): A re-evaluation of species limits in the genus *Atlapetes* based on mtDNA sequence data. – *Ibis* 141: 199-207.
- García-Moreno, J. & J.M.C. Silva (1997): An interplay between forest and non-forest South American avifaunas suggested by a phylogeny of *Lepidocolaptes* woodcreepers (Dendrocolaptinae). – *Studies Neotr. Fauna Envir.* 32: 164-173.
- Graves, G.R. (1980): A new species of metaltail hummingbird from northern Peru. – *Wilson Bull.* 92: 1-7.
- Graves, G.R. (1982): Speciation in the carbonated flower-piercer (*Diglossa carbonaria*) complex of the Andes. – *Condor* 84: 1-14.
- Graves, G.R. (1985): Elevational correlates in speciation and intraspecific geographical variation in plumage in Andean forest birds. – *Auk* 102: 556-579.
- Graves, G.R. (1988): Linearity of geographical range and its possible effect on the population structure of Andean birds. – *Auk* 105: 47-52.
- Graybeal, A. (1998): Is it better to add taxa or characters to a difficult phylogenetic problem? – *Syst. Biol.* 47: 9-17.
- Hackett, S.J. (1995): Molecular systematics and zoogeography of flowerpiercers in the *Diglossa baritula* complex. – *Auk* 112: 156-170.
- Haffer, J. (1997): Alternative models of vertebrate speciation in Amazonia: an overview. – *Biodiver. Conserv.* 6: 451-476.
- Hartl, D.L. & A.G. Clark (1997): Principles of population genetics. – Sinauer Ass. 304 pp.
- Heindl, M. & K.L. Schuchmann (1998): Biogeography, geographical variation and taxonomy of the Andean hummingbird genus *Metallura* GOULD, 1847. – *J.Orn.* 139: 425-473.
- Hooghiemstra, H., J.L. Melice, A. Berger & N.J. Shackleton (1993): Frequency spectra and paleoclimatic variability of the high-resolution 30-1345 ka FUNZA I pollen record (Eastern Cordillera, Columbia). – *Quatern. Sci. Rev.* 12: 141-156.
- Hooghiemstra, H. & T. van der Hammen (1998): Neogene and Quaternary development of the neotropical rain forest: the forest refugia hypothesis, and a literature overview. – *Earth-Science Reviews* 44: 147-183.
- Hubbell, S.P. (1999): A unified theory of biogeography and biodiversity. – Princeton Univ. Press.
- Hudson, R.R. (1990): Gene genealogies and the coalescence. – *Oxford Surveys Ecol. Biol.* 7: 1-44.
- Irwin, D.M., T.D. Kocher & A.C. Wilson (1991): Evolution of the cytochrome b gene of mammals. – *J. Mol. Evol.* 32: 128-144.
- Johnson, N.K., J.V. Remsen & C. Cicero (in press) Resolution of the debate over species concepts in ornithology: a new comprehensive biologic species concept. – 11 pp in: *Proc. 22nd Int. Orn. Congr., Durban.* – (SD-ROM, eds. Adams, N.J. & R.H. Slotow). – BirdLife South Africa, Johannesburg.

- Johnson, K.P. & M.D. Sorensen (1999): Phylogeny and biogeography of babbling ducks (genus: *Anas*): a comparison of molecular and morphological evidence. – *Auk* 116: 792-805.
- Klicka, J. & R.M. Zink (1997): The importance of recent ice ages in speciation: a failed paradigm. – *Science* 277: 1666-1669.
- Krabbe, N. & T.S. Schulenberg (1997): Species limits and natural history of *Scytalopus tapaculos* (Rhinocryptidae), with descriptions of the Ecuadorian taxa, including three new species. – pp. 74-88 in: *Neotropical Ornithology Honoring Ted Parker* (ed. Remsen, J.V.). – The American Ornithologists' Union, Washington D.C.
- Loeschcke, V., J. Tomiuk & S.K. Jain, eds (1994): *Conservation Genetics*. – Birkhäuser, Basel.
- Louette, M. (1992): Barriers, contact zones and subspeciation in central equatorial Africa. – *Bull. Brit. Orn. Club Centenary Suppl.* 112(A): 209-216.
- Lynch, J.D. (1988): Refugia. – pp. 311-342 in: *Analytical Biogeography* (eds Myers, A.A. & P.S. Giller). – Chapman & Hall, London.
- Maijer, S. & J. Fjeldså (1997): A new *Cranioleuca* spinetail from Bolivia, with description of a "leapfrog pattern" of geographical variation in the genus. – *Ibis* 139: 606-616.
- Mindell, D.P. & C.E. Thacker (1996): Rates of molecular evolution: phylogenetic issues and applications. – *Ann. Rev. Ecol. Syst.* 27: 279-303.
- Nielsen, K.K. & P. Arctander (submitted): Multiple mitochondrial pseudogenes with apparent recombination in a passerine genus. – *Mol. Phyl. Evol.*
- O'Neill, J.P. (1992): A general overview of the montane avifauna of Peru. – *Mem. Mus. Hist. Nat. UNMSM (Lima)* 21: 47-55.
- Parker, T.A., T.S. Schulenberg et al. (1985): The avifauna of the Huancabamba region, northern Peru. – pp. 160-197 in: *Neotropical Ornithology* (eds Buckley, T.A., S.F. Mercedes, E.S. Morton, R.S. Ridgely & F.G. Buckley). – The American Ornithologists' Union, Washington, D.C.
- Patton, J.L. & M.F. Smith (1992): mtDNA phylogeny and Andean mice: a test of diversification across ecological gradients. – *Evolution* 46: 174-183.
- Paynter, R.A., Jr. (1970): Subfamily Emberizinae. – pp. 3-214 in: *Checklist of Birds of the World, Vol. 8* (ed. Paynter, R.A.). Museum of Comparative Zoology, Cambridge Mass.
- Räsänen, M.E., J.S. Salo & R.J. Kalliola (1987): Fluvial perturbation in the western Amazon basin: regulation by long-term sub-Andean tectonics. – *Science* 283: 1398-1401.
- Remsen, J.V. (1984a): High incidence of 'leapfrog' pattern of geographic variation in Andean birds: implications for the speciation process. – *Science* 224: 171-173.
- Remsen, J.V. (1984b): Geographic variation, zoogeography, and possible rapid evolution in some *Cranioleuca* spinetails (Furnariidae) of the Andes. – *Wilson Bull.* 96: 515-523.
- Remsen, J.V. & W.S. Graves (1995a): Distribution patterns and zoogeography of *Atlapetes* brush-finches (Emberizidae) of the Andes. – *Auk* 112:

210-224.

- Remsen, J. V. & W. S. Graves (1995b): Distribution patterns of *Buarremon* brush-finches (Emberizidae) and interspecific competition in Andean birds. – *Auk* 112: 225-236.
- Rensch, B. (1929): Das Prinzip geographischer Rassenkreise und das Problem der Artbildung. – Borntraeger, Berlin.
- Roy, M. S., J. C. Torres-Mura & F. Hertel (1999): Molecular systematics of the South American tit tyrants (genus *Anairetes*) including *A. fernandezianus*. – *Mol. Phyl. Evol.* 11: 67-76.
- Roy, M. S., J. C. M. Silva, P. Arcander, J. García-Moreno & J. Fjeldså (1997): The role of montane regions in the speciation of South American and African birds. – pp. 325-343 in: *Avian Molecular Evolution and Systematics* (ed. Mindell, D. P.). – Academic Press, London.
- Servant, M., J. Maley, B. Turq, M.-L. Absy, P. Brenac, M. Fournier & M.-P. Lendry (1993): Tropical forest changes during the Late Quaternary in African and South American lowlands. – *Global and Planetary Change* 7: 25-40.
- Sibley, C. G. & J. C. Ahlquist (1990): *Phylogeny and classification of birds*. – Yale Univ. Press, New Haven.
- Simpson-Vuilleumier, B. (1971): Pleistocene changes in the fauna and flora of South America. – *Science* 173: 771-780.
- Smith, T. B., R. K. Wayne, D. J. Girman & M. W. Bruford (1997): A role for ecotones in generating rainforest biodiversity. – *Science* 276: 1855-1857.
- Stepien, C. A. & T. D. Kocher (1997): Molecules and morphology in studies of fish evolution. – pp. 1-11 in: *Molecular systematics of fishes* (eds. Kocher, T. D. & C. A. Stepien). – Acad. Press, London.
- Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III & D. K. Moskovits (1996): *Neotropical Birds. Ecology and Conservation*. – Univ. Chicago Press, Chicago.
- Templeton, A. R. & B. Read (1984): Factors eliminating inbreeding depression in a captive herd of Speke's gazelle (*Gazella spekei*). – *Zoo Biol.* 3: 177-199.
- Traylor, M. A. (1985): Species limits in the *Ochthoeca diadema* species-group (Tyrannidae). – *Ornithol. Monogr.* 36: 430-442.
- Volker, G. (1999): Molecular evolutionary relationships in the avian genus *Anthus* (pipits: Motacillidae). – *Mol. Phyl. Ecol.* 11: 84-94.
- Vuilleumier, F. (1969): Pleistocene speciation in birds living in the high Andes. – *Science* 223: 1179-1180.
- Vuilleumier, F. (1984a): Zoogeography of Andean birds: two major barriers, and speciation and taxonomy of the *Diglossa carbonaria* superspecies. – *Nat. Geogr. Soc. Res. Reports* 16: 713-731.
- Vuilleumier, F. (1984b): Patchy distribution and systematics of *Oreomanes fraseri* (Aves, Coerebidae) of the Andean *Polylepis* woodlands. – *Am. Mus. Novit.* No. 2777.
- Vuilleumier, F. & D. Simberloff, D. (1980): Ecology vs. history as

- determinants of patchy and insular distributions in high Andean birds. – pp. 235-379 in *Evolutionary Biology*, Vol. 12 (eds. Hecht, M.K., W.C. Steere & B. Wallace). – Plenum, New York.
- Waddell, P.J., Y. Cao, M. Hasegawa & D.P. Mindell (1999): Assessing the Cretaceous superordinal divergence times within birds and placental mammals using whole mitochondrial protein sequences and an extended statistical framework. – *Syst. Biol.* 48: 119-137.
- Walter, G.H. & H.E.H. Paterson (1994): The implications of palaeontological evidence for theories of ecological communities and species richness. – *Aust. J. Ecol.* 19: 241-250.
- Wijnnga, V.M. (1995): A first approximation of montane forest development during the late Tertiary in Colombia. – pp. 23-34 in: *Biodiversity and conservation of Neotropical montane forests* (eds. Churchill, S.P., H. Balslev, E. Forero & J.L. Luteyn). – The New York Botanical Garden: 23-34.
- Williams, P.H. (1994): *WORLDMAP*. Priority areas for biodiversity. Ver. 3. Privately distributed computer software and manual. – The Natural History Mus., London.
- Zimmer, J.T. (1951): *Studies of Peruvian birds* No. 60. The genera *Heliodoxa*, *Phlogophilus*, *Urosticte*, *Polyplancta*, *Adelomyia*, *Coeligena*, *Ensifera*, *Oreotrochilus*, and *Topaza*. – *Amer. Mus. Novit.* 1513: 1-45.

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Biogeography, geographical variation, and taxonomy of the Neotropical hummingbird genus *Polyerata* Heine, 1863 (Aves: Trochilidae)

André-A. Weller

Abstract: Recent studies on distribution and morphological characters of the Neotropical hummingbird genus *Amazilia* indicate a polyphyletic origin of this taxon, thus contradicting the presently assumed monophyly of *Amazilia*. One of the proposed subgenera, *Polyerata* (Heine, 1863), is here regarded as distinct at the generic level. These findings are based on recent biogeography and geographical variation studies. It is hypothesized that the six species of the current *Polyerata* group are derived from a common ancestor that originated in northern South America.

Key words: *Amazilia*, *Polyerata*, Trochilidae, biogeography, taxonomy, Neotropics

Introduction

The genus *Amazilia*, Trochilidae, is considered by recent reviewers the largest taxon of the hummingbird subfamily Trochilinae, comprising 29 (Peters 1945) to 33 (Wolters 1982) species. Its current distribution ranges from the southern Nearctic region (southwestern USA) to the southern Neotropics (southward to Bolivia, Argentina, and Uruguay). In previous studies, classification was based on general similarity and distributional aspects. Existing morphological patterns within *Amazilia* have often been neglected, even by Simon (1921) and Peters (1945), either by creating new genera (Simon) or including other species groups (e.g., *Polyerata*, *Saucerottia*) as subgenera in the taxon *Amazilia* (Peters).

A recent study (Weller 1998) indicates that several members of the current subgenus *Polyerata* can be distinguished from *Amazilia* by plumage patterns and zoogeographic aspects. As a taxonomic consequence I propose that *Polyerata* represents a valid genus.

Material and methods

Altogether 1116 specimens of all taxa of *Polyerata* were compared with those of *Amazilia* and studied for geographical variation. For the evaluation of colour characters I examined specimens under natural light conditions and by means of a magnifying lamp ($\times 10$). Morphometric data were obtained using a digital caliper (measured to the nearest 0.5 mm). Range maps were drawn based on distributional data derived from skin specimens and literature (Sánchez Osés 1995). Collecting sites were located using ornithological gazetteers (Paynter 1982, 1985, 1989, Paynter & Traylor 1977, 1981, 1983, 1991, Stephens & Traylor 1985) and diverse travel maps.

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Results

Taxonomy and distribution of *Polyerata*

The genus *Polyerata* was initially separated from *Damophila* (Gould 1861) by Heine (1863), who designated *P. amabilis* as type species. Later taxonomists, such as Elliot (1878) and Hartert (1900), often placed *Polyerata* species in the genus *Agyrtria*. Simon (1921) erroneously included several species in the genera *Damophila*, *Arenella* (nom. nov.), and *Chionomesa* (nom. nov.). More recently, Peters (1945) merged *Agyrtria* and *Polyerata* under the latter name as a subgenus of the older taxon *Amazilia* (Lesson 1843). This classification has been maintained in various subsequent revisions (e.g., Zimmer 1950, Wolters 1982, Sibley & Monroe 1990).

My studies of the currently recognized genus *Amazilia* (Weller 1998) suggest that six species should be separated as members of the genus *Polyerata*: *P. fimbriata*, *P. lactea*, *P. amabilis*, *P. rosenbergi*, *P. boucardi*, and *P. luciae*. The last three species are monotypic, the others polytypic. *Polyerata* ranges from interior Central America to southeastern South America.

1. *Polyerata fimbriata* (Gmelin, 1788)

This most widespread, polytypic member of the genus is found exclusively in South America, from eastern Colombia to southeastern Brazil (plate 1). Seven subspecies are recognized (from N to S):

- P. f. elegantissima* (Todd, 1942): N and NW Venezuela, adjacent parts of E Colombia;
- P. f. fimbriata* (Gmelin, 1788): NE Venezuela to Guyana and N Brazil (to Amapá);
- P. f. apicalis* (Gould, 1861): E Colombia at base of Andes and adjacent lowlands;
- P. f. fluviatilis* (Gould, 1861): SE Colombia to NE Ecuador;
- P. f. laeta* (Hartert, 1900): NE Peru;
- P. f. nigricauda* (Elliot, 1878): C and E Brazil from Bahia to São Paulo, E Bolivia;
- P. f. tephrocephala* (Vieillot, 1818): SE Brazil from Espírito Santo to Rio Grande do Sul.

2. *Polyerata lactea* (Lesson, 1829)

Besides *P. fimbriata*, this species is the only one that occurs exclusively east of the Andes in South America. Unlike *P. fimbriata* it shows a highly scattered mosaic-like distribution,

mainly south of the Amazon basin (plate 1). Three subspecies are recognized (from N to S):

- P. l. zimmeri* (Gilliard, 1941): tepuis of SE Venezuela;
- P. l. bartletti* (Gould, 1866): tropical zone from E Ecuador to N Bolivia;
- P. l. lactea* (Lesson, 1829): C and SE Brazil.

Plate 1: Distribution of *Polyerata* species in South America based on data obtained from skin specimens. Upper left: *P. rosenbergi*; upper right: *P. fimbriata*; lower birds: *P. lactea*; female (left) and male (right)

Plate 2 (next page): Distribution of *Polyerata* species in Central and northwestern South America based on data obtained from skin specimens. Upper birds: *P. luciae*; mid birds: *P. boucardi*; lower birds *P. amabilis*; female (left) and male (right)





3. *Polyerata rosenbergi* (Boucard, 1895)

This monotypic species is confined to the tropical lowland rain forests from W Colombia to NW Ecuador (plate 1).

4. *Polyerata amabilis* (Gould, 1851)

P. amabilis is found both in Central and South America (plate 2). Several reviewers have regarded the race *decora* as a distinct allospecies (e.g., Wetmore 1968, Stiles et al. 1989, Sibley & Monroe 1990). The race *costaricensis* (Todd 1942) was described from the northwestern range of the species but is not recognized here as colour variations in the dorsal plumage occur in the morphologically heterogeneous nominate form. Two subspecies are recognized (from N to S):

P. a. amabilis (Gould, 1851): NE Nicaragua to NE Colombia and W Ecuador;

P. a. decora (Salvin, 1891): SW Costa Rica to W Panamá (Chiriqui).

5. *Polyerata boucardi* (Mulsant, 1877)

P. boucardi is a monotypic endemic of Costa Rica, restricted to mangrove areas along the Pacific Coast from Gulf of Nicoya to Rio Grande de Terraba (plate 2).

6. *Polyerata luciae* (Lawrence, 1867)

This monotypic taxon occurs only in thorn forests of N and C Honduras (plate 2) where it has become a vulnerable species.

Morphology and geographical variation

Variation in plumage characters

All members of the genus share the golden to bronze-green dorsal coloration and tail, a glittering gorget or throat patch and a grayish to whitish abdomen. In part, these colour patterns differ strongly from those of other species groups within the *Amazilia* complex. For example, species of the *Amazilia tzacatl* group (including, e.g., *A. amazilia*, *A. rutila*, *A. yucatanensis*) have a rufous tail and a rufous to brownish-grayish abdomen. Furthermore, birds of the *Agyrtria* group (e.g., *A. leucogaster*, *A. franciae*) show whitish underparts and more or less contrasting, often glittering caps. Sexual dimorphism in *Polyerata* species is slight; females usually have more whitish fringes or discs on the throat.

P. fimbriata shows the strongest geographical variation within the group, with a gorget that is glittering golden (northern, eastern subpopulations) to bluish green (western subpopulations *fluviatilis*, *laeta*). Unlike *P. fimbriata*, *P. lactea* has a violet-blue gorget. Both taxa have in common the pure white center of belly and abdomen (reduced in *P. l. bartletti*). *P. amabilis* and *P. rosenbergi* are violet-blue only on the throat, a character reduced in females. The abdominal region is grayer. As apomorphic characters, *P. amabilis* has a golden to bronze-green glittering crown and a bronzish chin.

A different throat coloration occurs in *P. boucardi* (golden green) and *P. luciae* (turquoise-green). The abdomen is more grayish white and there are light green (*boucardi*) to grayish green rectrices (*luciae*).

Morphometric variation

Polyerata spp. are medium-sized trochilids (9–11 cm, 4–7 g) with straight or slightly decurved, medium-length bills (20–25 mm). The South American taxa *P. fimbriata* and *P. lactea* are morphometrically very similar. Within *P. fimbriata*, the bill length increases from eastern to western subpopulations in the Amazon basin (*P. f. fimbriata*, *P. f. nigricauda*: 19–21 mm; *P. f. apicalis*, *P. f. fluviatilis*: 23–24 mm; averages for males). *P. f. tephrocephala* is the largest form, with a bill length of 23 mm and a wing length of 59 mm (males). In *P. lactea*, the wing is longer in *P. l. bartletti* and *P. l. zimmeri* (54–57 mm, males) than in the nominate race (52–53.5 mm). *P. lactea* and *P. amabilis* are similar in measurements.

Although *P. amabilis* and *P. rosenbergi* occur in sympatry, they differ in bill length (*P. a. amabilis*: 18.5–19.5 mm; *P. rosenbergi*: 19–21.5 mm, males). However, southern subpopulations of the latter have shorter bills. In *P. amabilis*, *P. a. decora* has a significantly longer bill (22.5–24 mm, both sexes) than the nominate race.

The Central American taxa *P. boucardi* and *P. luciae* differ from *P. amabilis* chiefly in length of outer rectrices (males of *P. boucardi*/*P. luciae*: 34–34.5 mm; *P. a. amabilis*/*P. a. decora*: 29–30.5 mm) which are longer than the inner ones by 6.0 mm in *P. boucardi*/*P. luciae* vs. 1–3.5 mm in *P. amabilis*. Moreover, *P. luciae* has a longer bill (22 mm, males) than *P. boucardi* (20 mm, males).

Discussion

When considering biogeographical aspects of the Neotropical fauna and flora, it has often been suggested that refuges played an important role in speciation processes (e.g., for birds see Haffer 1967, 1969, 1979; for butterflies, Brown & Mielke 1972; for plant families, Prance 1973). Alternatively, several reviewers found that range patterns of some bird species are correlated with river systems, implying that rivers are potential barriers to gene flow (riverine theory; e.g., Hellmayr 1910, Sick 1967, Salo et al. 1986).

Based on distributional data and morphological patterns in *Polyerata*, I suggest elsewhere (Weller 1998) that the evolutionary center of the genus is in South America. Morphometric and colour characters indicate that plesiomorphic characters are found in *P. fimbriata* and *P. lactea*. Presumably, both taxa are derived from a common ancestor by ecological segregation (tropical vs. subtropical habitats) prior to the Pleistocene. Probably *P. fimbriata* evolved in rain forest areas north of the Amazon (Guyana shield), and *P. lactea* in semideciduous subtropical forest of southeastern Brazil or the Andes.

Subsequently, the radiation of *P. fimbriata* was bidirectional as subpopulations invaded the western Amazon basin and Venezuela, and others reached central (*P. f. nigricauda*) and eastern Brazil (*P. f. tephrocephala*). It seems possible that either the development of the Amazon river system or Pleistocene flooding of the lower Amazon basin separated the northern and southern subpopulations (compare Willis 1969); however, they have come in secondary contact along the river more recently (zone of intergradation of *P. f. fimbriata* / *f. nigricauda*).

If *P. lactea* originated in southeastern Brazil, westward emigration could have resulted in invasion of the submontane zone of the Andes (Peru, Bolivia: *P. l.*

bartletti) and the Pantepui region of southeastern Venezuela (*P. l. zimmeri*). As *P. l. bartletti* is a very divergent form in colour, and *P. l. zimmeri* similar to *P. l. lactea*, there could have been "leapfrog" evolution (Renssen 1984). Considering the origin of the taxa west of the Andes and in Central America, I hypothesize that this group was derived from the eastern Andean *P. lactea* population. Based on present-day ecological requirements, a proto-*amabilis-rosenbergi* associated with montane rain forest could have crossed the Andes either in S Colombia or S Ecuador. Subsequently, the precursors of both taxa were isolated in different refuges (*P. rosenbergi*: Chocó Center; *P. amabilis*: Panamá Center; see Müller 1973). For *P. amabilis decora*, it is postulated that it developed in a Pleistocene submontane forest refuge of Cordillera de Talamanca.

On the basis of morphological similarities, the *P. boucardi-luciae* group possibly evolved from *P. amabilis* during the mid-Pleistocene. Strong habitat differences (*P. boucardi*: mangroves; *P. luciae*: thorn forest) in the current taxa indicate ecological segregation of the *boucardi-luciae* precursor populations that, however, once may have been connected due to greater habitat tolerances. The present, rather relictual populations of both species may be caused by man-made influences (e.g., habitat fragmentation) as well as interspecific competition (*amabilis-boucardi*). As a consequence, *P. boucardi* and *P. luciae* are two of the rarest and most endangered trochilids of Central America (Collar et al. 1992).

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References

- Boucard, A. (1895): Genera of humming birds. – Humming Bird 5: 1-402.
 Brown, K.S., Jr. & O.F.F. Mielke (1972): The Heliconians of Brazil (Lepidoptera: Nymphalidae). Pt. II. Introduction and general comments, with a supplementary revision of the tribe. – Zoologica, N. Y. Zoological Society.

- Collar, N.J., L.P. Gonzaga, N. Krabbe, A. Madroño-Nieto, L.G. Naranjo, T.A. Parker, III & D.C. Wege (1992): Threatened birds of the Americas: The ICBP/IUCN Red Data Book, third edition, part 2. – International Council for Bird Preservation, Cambridge, U.K.
- Elliot, D.G. (1878): A classification and synopsis of the Trochilidae. – *Smithson. Contrib. Know.* 317: 1-277.
- Gilliard, E.T. (1941): The birds of Mt. Auyan-Tepui, Venezuela. – *Bull. Amer. Mus. Nat. Hist.* 77: 439-508.
- Gmelin, J.F. (1788): *Syst. Naturae*, ed. 13, 1: 448.
- Gould, J. (1851): On some new species of Trochilidae. – *Proc. Zool. Soc. London* 19: 115-116.
- Gould, J. (1861): An introduction to the Trochilidae, or family of humming-birds. – London.
- Gould, J. (1866): pp 175-201 in: Catalogue of birds collected by Mr. E. Bartlett on the River Ucayali, Eastern Peru, with notes and descriptions of new species (eds. Sclater, P.L. & O. Salvin). – *Proc. Zool. Soc. London* 34.
- Haffer, J. (1967): Speciation in Colombian forest birds west of the Andes. – *Amer. Mus. Novit.* 2294: 1-57.
- Haffer, J. (1969): Speciation in Amazonian forest birds. – *Science* 165: 131-137.
- Haffer, J. (1979): Quaternary biogeography of tropical lowland South America. – pp. 107-140 in: *The South American Herpetofauna: its origin, evolution, and dispersal* (ed. Duellman, W.) – The University of Kansas, Lawrence.
- Hartert, E. (1900): Trochilidae. *Das Tierreich*. 9. Lieferung. – R. Friedländer & Sohn, Berlin.
- Heine, F. (1863): Trochilidica. – *J. Ornithol.* 11: 173-217.
- Hellmayr, C.E. (1910): The birds of the Rio Madeira. – *Novit. Zool.* 17: 257-428.
- Lawrence, G.N. (1867): Descriptions of six new species of birds of the families Hirundinidae, Formicariidae, Tyrannidae, and Trochilidae. – *Ann. Lyc. New York* 8: 400-405.
- Lesson, R.P. (1829): *Histoire naturelle des oiseaux-mouches*. – Arthus Bertrand, Paris.
- Lesson, R.P. (1843): *Echo du Monde Sav.*, col. 757.
- Müller, P. (1973): The dispersal centres of terrestrial vertebrates in the Neotropical realm. A study in the evolution of the Neotropical biota and its native landscape. – *Biogeographica* 2: 1-244.
- Mulsant, E. (1877): Descriptions des espèces nouvelles des Trochilidés. – *Ann. Soc. Linn. Lyon*: 6.
- Paynter, R.A., Jr. (1982): *Ornithological Gazetteer of Venezuela*. – Mus. Comp. Zool., Cambridge, Mass.
- Paynter, R.A., Jr. (1985): *Ornithological Gazetteer of Argentina*. – Mus. Comp. Zool., Cambridge, Mass.

- Paynter, R.A., Jr. (1989): Ornithological Gazetteer of Paraguay. 2nd edition. – Mus. Comp. Zool., Cambridge, Mass.
- Paynter, R.A., Jr. & M.A. T aylor, Jr. (1977): Ornithological Gazetteer of Ecuador. – Mus. Comp. Zool., Cambridge, Mass.
- Paynter, R.A., Jr. & M.A. T aylor, Jr. (1981): Ornithological Gazetteer of Colombia. – Mus. Comp. Zool., Cambridge, Mass.
- Paynter, R.A., Jr. & M.A. T aylor, Jr. (1983): Ornithological Gazetteer of Peru. – Mus. Comp. Zool., Cambridge, Mass.
- Paynter, R.A., Jr. & M.A. T aylor, Jr. (1991): Ornithological Gazetteer of Brazil. – Mus. Comp. Zool., Cambridge, Mass.
- Peters, J.L. (1945): Check-list of birds of the world. Vol. 5. – Cambridge, Mass.
- Prance, G.T. (1973): Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. – Acta Amazonica 3: 5-28.
- Remsen, J. V. (1984): High incidence of “leapfrog” patterns of geographic variation in Andean birds: implication for the speciation process. – Science 224: 171-173.
- Salo, J., R. Kalliola, I. Häkinnen, Y. Mäkinen, P. Niemelä, M. Pukakka, & P.D. Coley (1986): River dynamics and the diversity of Amazon lowland forest. – Nature 322: 254-258.
- Sánchez Osés, C. (1995): Distribución geográfica de la familia Trochilidae (Aves: Apodiformes) en Venezuela con algunas implicaciones biogeográficas. – Unpubl. Master's thesis, Universidad Central de Venezuela, Caracas.
- Salvin, O. (1891): Descriptions of new species of Upupæ and Trochili in the collection of the British Museum. – Ann. Nat. Hist. 7: 374-378.
- Sibley, C.G. & B.L. Monroe (1990): Distribution and taxonomy of birds of the world. – Yale University Press, New Haven.
- Sick, H. (1967): Rios e enchentes na Amazonia como obstáculo para a avifauna. – pp. 495-520 in: Atas do simpósio sobre a biota Amazônica, 5 (Zool.) (ed. Lent, H.). – Conselho Nacional de Pesquisas, Rio de Janeiro.
- Simon, E. (1921): Histoire naturelle des Trochilidés (synopsis and catalogue). – Encyclopédie Roret, L. Mulo, Paris.
- Stiles, F.G., A.F. Skutch & D. Gardner (1989): A guide to the birds of Costa Rica. – Christopher Helm. Bromley, London.
- Stephens, L. & M.A. T aylor, Jr. (1985): Ornithological Gazetteer of the Guianas. – Mus. Comp. Zool., Cambridge, Mass.
- Todd, W.E.C. (1942): List of hummingbirds in the collection of the Carnegie Museum. – Ann. Carnegie Mus. 29: 271-370.
- Vieillot, J.L.P. (1818): Nouvelle dictionnaire d'histoire naturelle, 13. – Paris.
- Weller, A.-A. (1998): Biogeographie, geographische Variation und Taxonomie der Gattung *Amazilia* (Aves: Trochilidae). – Unpubl. doctoral thesis, Rhein. Friedrich-Wilhelms-Universität Bonn.

- Wetmore, A. (1968): The birds of the Republic of Panamá. Part 2. – Columbidae (Pigeons) to Picidae (Woodpeckers). – Smithsonian Institution Press, Washington, D.C.
- Willis, E.O. (1969): On the behavior of five species of *Rhegmatorhina*, ant-following birds of the Amazon basin. – Wilson Bull. 81: 363-395.
- Wolters, H.E. (1982): Die Vogelarten der Erde. – Parey, Hamburg.
- Zimmer, J.T. (1950): Studies of Peruvian birds. No. 59. The genera *Polytmus*, *Leucippus*, and *Amazilia*. – Amer. Mus. Novit. 1475: 1-27.

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Taxonomic considerations on the genus *Orestias* Valenciennes, 1839 (Teleostei: Cyprinodontidae) of the Chilean Altiplano

Wolfgang Villwock, Ulrike Sienknecht & Arne Lüssen

Abstract: The present distribution of the teleost genus *Orestias* Valenciennes, 1839, endemic to the Altiplano, can be explained by the extent of the lake and river systems during the Plio- and Pleistocene. The last main revisions of the genus defined 20 and 43 species respectively. Investigations by Villwock and co-workers have shown that it is rather unlikely that such a number of species might have evolved under the given historic, geographic and ecological conditions. Additionally, some of the characters used for the separation of the species are highly variable. Recently, crossbreeding experiments with four *Orestias*-species were started to clarify their intrageneric relationships. All F₁ are fertile and as far as already produced - the further offspring too.

According to all aspects and results of the different investigations the four "species" of the Chilean Altiplano belong to one species, *Orestias agassizii* Cuvier & Valenciennes, 1846.

Key words: *Orestias*, *Orestias-agassizii* assemblage, crossbreeding experiments, Altiplano, South America

Introduction

The cyprinodontids of the genus *Orestias* Valenciennes, 1839 are the only endemic and autochthonous teleosts inhabiting the remnants of ancient water bodies in the Altiplano of Perú, Bolivia and Chile, with its center in recent Lake Titicaca (fig.1). Tchernavin (1944) ranked the genus *Orestias* as an own subfamily (family Cyprinodontidae) while Costa (1997) reduced it to a tribe Orestiini within the subfamily Cyprinodontinae. We prefer the differentiation suggested by Tchernavin because (1) he published the last, in many aspects most convincing revision of the *Orestias* species-group, and (2) because the question of the real interrelationship with other cyprinodontid units seems to be unsolved and open to further discussion – despite Costa's very thorough morphological and morphometric investigations. According to our view, Costa's phyletic and biogeographic conclusion of three different, equally ranked tribes also allows the postulation of three different subfamilies (see fig.2) – a point of view not that far from Tchernavin's and our own. This view, however, is contrary to the opinion of Parenti (1984) or Parker & Kornfield (1995), who believe that a sister-group relationship exists between *Orestias* and Anatolian representatives of Old World Aphanini. We will not discuss here in detail why we are sceptical of Parenti's hypothesis. However, her postulation of a total of 43 different species of *Orestias* (24 of them solely within the borders of recent Lake Titicaca!) is not feasible, neither on the basis of many of the characters she used (c.f. comments by Müller 1993, Villwock & Sienknecht 1993) nor of events in the historic development from ancient to recent Altiplano

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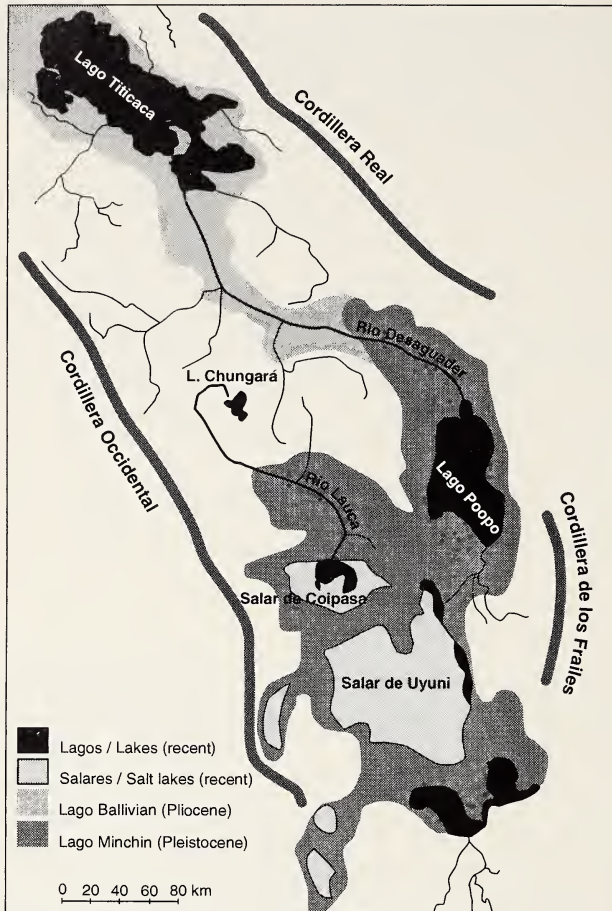


Fig.1: Map of the ancient water body and its recent remnant in the Altiplano (draft by Sienknecht, PC-drawing by Stiewe)

water bodies (see Moon 1939, Newell 1949, Ahlfeld & Branisa 1960, Zeil 1979, 1984, Wörner et al. 1988, Kött et al. 1995) (fig.1). Whichever is true, the orestiine cyprinodontids are as a whole one of the “isolated vertebrate communities in the tropics” (see fig.2C).

We will concentrate on some aspects resulting from own investigations on a geographically restricted group of *Orestias* in the Chilean part of the Altiplano which has been said to belong to four different species: *O. parinacotensis*, *O. laucaensis* (Arratia 1982), *O. ascotanensis* (Parenti 1984) and *O. chungarensis* (Vila & Pinto 1986) (fig.3; fig. 4: points 1, 2, 3 and 7).

In 1991, Villwock and Sienknecht collected fishes of three additional populations: from the rivers Isluga (fig.4: 4) and Collacagua (fig.4: 5) and from springs at the eastern border of the Salar de Huasco (fig.4: 6). These new points are located between - but not actually connected with - the three northern “species” and “*O. ascotanensis*” in the south of the Chilean Altiplano. These populations (and probably more may exist) were only named according to their locations, and not described as new species, because of reasonable suspicion that they might be the



Fig.2: Assumed phylogeny of Cyprinodontinae (after Costa 1997):

A: Old World Aphaniini – B: New World Cyprinodontini – C: New World Orestiini

nearest relatives of an already known species: *Orestias agassizii*¹ Cuvier & Valenciennes, 1846, including the four above mentioned “species”. This taxonomic

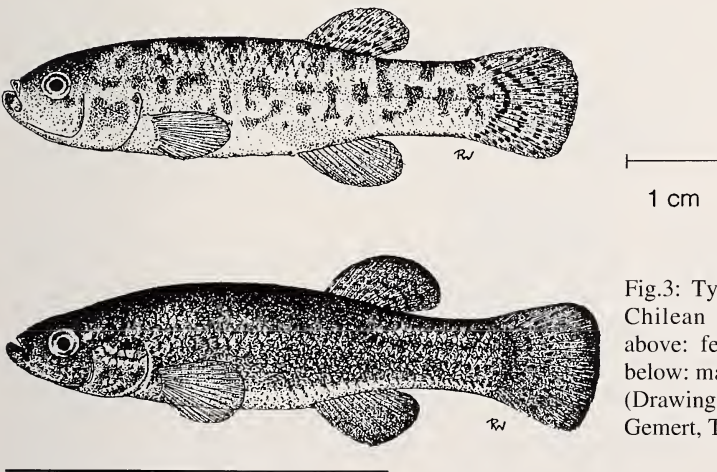


Fig.3: Typical representatives of Chilean *Orestias*-populations; above: female from Rio Lauca; below: male from Rio Isluga. (Drawings by Ruud Wildekamp, Gemert, The Netherlands)

¹) According to Eschmeyer (1998) the correct name should be “agassizii”, whereas the most commonly used name “agassii” (introduced by Tchernavin 1944) is a typesetting error

concept derived from the common geological history (see above) and the supposed young separation of their present habitats in the Chilean Altiplano, i.e. own suggestions of an approximate age of separation of less than 15 000 years B.P. (Villwock et al. 1987; based on ^{14}C -aging reported by Geyh, Niedersächsisches Landesamt für Bodenforschung, March 1986: $11\,730 \pm 100$ ys). This was meanwhile confirmed by geological investigations, e.g. Francis & Self (1987): 15 000 to 17 000 ys, Harmon et al. (1987): < 15 000 ys, Wörner et al. (1988): 13 500 ys and others. Additional results concerning the age of Chilean Altiplano lakes and their fauna were published by Villwock & Sienknecht (1993, 1995, 1996) and by Schwalb et al. (1999).

The results of the comparison of the four species descriptions given by Arratia, Parenti and Vila & Pinto (see above), with observations from our own investigations (including the thesis data by Thomann 1990), are presented in the following paragraphs.



Fig.4: The distribution of Chilean *Orestias*
(Draft Sienknecht, PC-drawing Stiewe)

A - Lago Titicaca; B - Lago Poopo; C - Salar de Surire; D - Salar de Coipasa; E - Salar de Uyuni; F - Salar d'Ascotán
1 - Lago Chungará (LC); 2 - Laguna de Parinacota (LP); 3 - Rio Lauca (RL); 4 - Rio Isluga (RI); 5 - Rio Collacagua (RC); 6 - Salar de Huasco (SH); 7 - Salar d'Ascotán (SA)

Morphometric and meristic characters

Head-length / standard-length

Thomann (1990) reports on some basic data such as the main morphometrics (body-indices) and meristic characters (number of fin rays in the dorsal and anal fins) which he found in a total of 858 specimens, among them 419 of the population of Lago Chungará (fig.2:1), 122 of Parinacota (fig.2:2), 172 of Lauca (fig.2:3), 25 of Huasco (fig.2: 6) and 110 of Salar d'Ascotán (fig.2:7). One of the most commonly used metric characters for discriminating different species is that of the coefficient between head-length and standard-length (see fig.5: B/A).

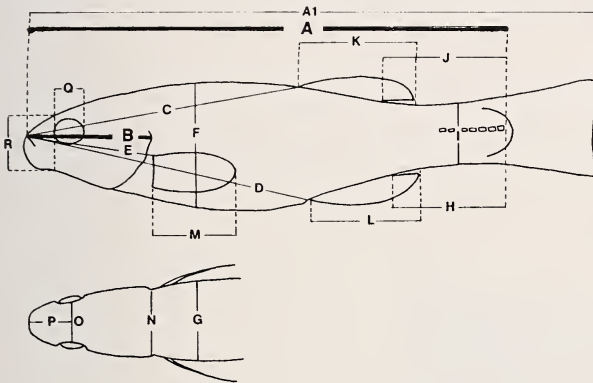


Fig.5: Distances to be measured (after Lauzanne 1981)

These indices do not show any significant differences between these five compared localities (Thomann 1990: 63, table 14). Other metric data, such as body height (fig.5: F) or body width (fig.5: G) are not very reliable because they depend on nutritional condition, stage of maturity (differing between female and male) and many other physiological conditions of the studied specimens.

The main morphometric similarities of the four "species" and the population of Salar de Huasco were calculated from random samples of 25 specimens of each population. The results led to the dendrogram shown below, reflecting the narrow relationship between the Chilean *Orestias* tested (fig.6):

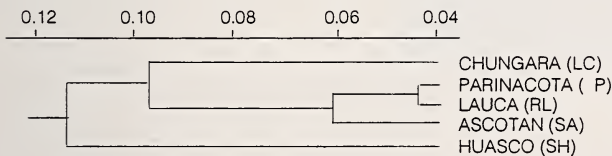


Fig.6: Morphometric similarities (Thomann 1990)

Moreover, the average values of Thomann correspond to those given by Lauzanne 1982: 42) and Loubens & Sarmiento (1985) concerning *O. agassizii* from Lago Pequeño (the smaller part of Lake Titicaca) and the Lago Grande (main Lake Titicaca). This correspondence shows a close relationship in these important characters between *Orestias agassizii* and the five cited Chilean populations, an assumption that was first made by Villwock & Thomann (1987) and again by Villwock & Sienknecht (1993), based on their own numerous measurements.

Finrays in the dorsal and anal fins

A similar result is obtained from the comparison of meristic characters, e.g. the variability of finrays in the dorsal and anal fins, which do not differ significantly neither within the four northern Chilean "species" (inclusive the Huasco-population: Thomann 1990) nor between the latter and *O. agassizii* from different parts of its range (Lauzanne 1982 and own collections: Villwock & Sienknecht 1993). The average values of the dorsal fin (D) range from 13.3 (Lauca) to 15.2 (Chungará); the average values for the anal fin (A) range from 13.5 (d'Ascotán) to 15.0 (Chungará and Huasco). These values are again within the normal distribution of *O. agassizii* sensu Lauzanne (1982).

Scales and scalation

The number of scales and the degree of scalation are no useful characters for species discrimination since scale reductions occur in all oreitiine cyprinodonts. Moreover, scales show a high variability in counts (and size) within the same popu-

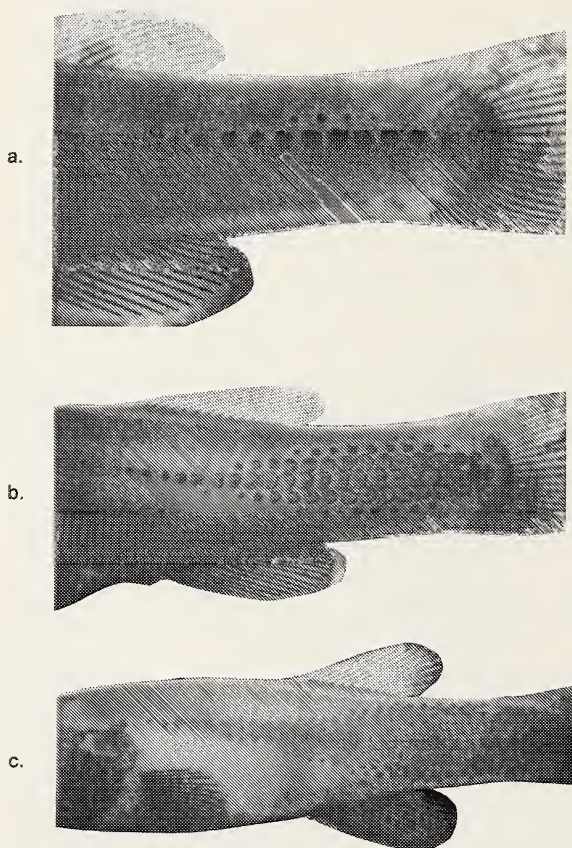


Fig.7: Different stages of scale development (alizarine-S-staining)

a: TL 18-19mm; **b:** TL 20-21mm; **c:** TL 25-26mm (Lüssen 1998)

lation, as it is generally known for comparable characters that undergo reductions (Villwock 1963). Therefore already Tchernavin (1944) stated correctly that “the number of scales in *Orestias* varies widely and a difference of two or three scales obtained in examining a few specimens cannot be considered specific” (p. 148).

In cases of irregularities of the scalation, another aspect should also be considered: Lüssen (1998) demonstrated that the number of scales in the longitudinal line, and especially those in the transversal line (corresponding with differences of the extent of naked parts of the body), depend directly on growth (and age) (figs. 7a-c). Accordingly, Tchernavin’s statement should be completed by the reservation that in cases of reduced scalation only specimens of about the same size should be used for counts of scales. If specimens of the same size are not available this character should not be used for species discrimination at all.

Aspects of growth, manifestation of characters and sexual maturation

As just pointed out, some of the morphometric and meristic characters depend directly on the ontogenetic stage. However, this is not only true with respect to reduction characters (as scales and scalation) but also to sexual maturity. Normally, sexual maturity is or may be used as synonym for being “full grown” or “adult”. This statement may work in general, but does not apply in the genus *Orestias*: sexual maturity will be reached in the Chilean group at an age of about 9 months, their full-grown stage however at not below two years (controlled in the aquarium). Also, within this period and phenotypical variation the scalation will continue to become individually completed. In other words, sexual maturity of the specimens and their special scalation characters cannot be used for species discrimination. This appears to be one of Parenti’s (1984) chief errors when she created at least some of her new species for Lake Titicaca (see also Müller 1993).

Feeding habits as a tool for species distinction

Vila & Pinto (1986) and Pinto & Vila (1987) were asking in the context of their species description for special feeding habits; however they could not state significant differences in food consumption. Those differences described by Thomann (1990) obviously depended on seasonal differences in food availability. There is no doubt that the Chilean *Orestias* populations consist of omnivorous specimens – as does *O. agassizii* (Villwock (1966), Lauzanne (1982), Loubens & Sarmiento (1985).

Genetic aspects in species discrimination

Number of chromosomes

The first counts were reported by Lueken (1962), who found in samples of *O. luteus* and *O. agassizii* the haploid number of $n=24$ ($2n=48$). Arratia (1982) found the same result with respect to *O. parinacotensis*. The other new species described by Arratia, *O. laucaensis*, has $2n=51$ chromosomes in females and $2n=52$ in males – the discriminating feature between the two species. In general, it is not very rare in fishes that males and females differ by one chromosome; however, normally the males have the lower counts: e.g., goodeid males $2n=41$, females $2n=42$ (Uyeno & Miller 1972, Uyeno et al. 1973). According to general chromosomal investigations on fishes (Makino 1951) and many

comparative studies since then (e.g., Nogusa 1960, Roberts 1967, Gyldenholm & Scheel 1971, Foerster & Anders 1977, Rab et al. 1987, Vitturi et al. 1996), including some contributions with special concern to oviparous cyprinodonts (cf. Karbe 1961, Gold et al. 1980, Vitturi et al. 1995) the by far most common karyotype in fishes is $2n = 48$ chromosomes.

Preliminary enzyme investigations

In addition to the facts discussed above, Thomann (1990) initiated the first electrophoretic investigations on the Chilean *Orestias* from Lago Chungará, Parinacota and Rio Lauca (see fig.4), using tissue homogenates, separated in vertical starch gels. Twelve enzymes were assayed (24 loci): on the basis of these results (see Thomann 1990: table 29, p.99) the author calculated the genetic similarities according to Nei (1972), illustrated in the following scheme and dendrogram:

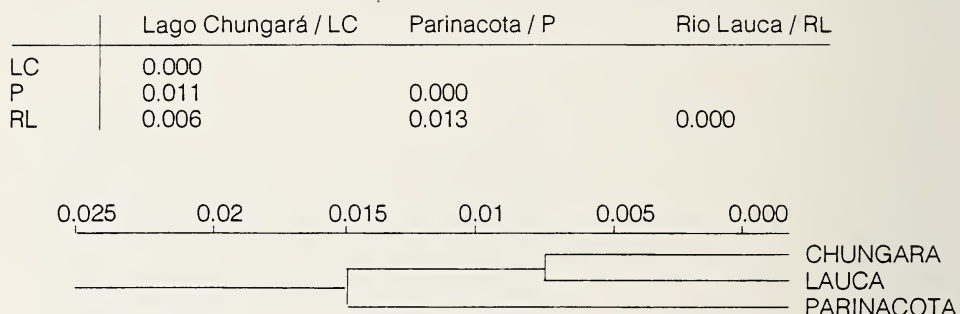


Fig.8: Evaluated genetic distances according to Nei (1972) (above) and dendrogram of genetic similarities (below) (Thomann 1990)

According to this study, the genetic distance between the three tested Chilean *Orestias*, *O. chungarensis*, *O. parinacotensis* and *O. laucaensis* is even beyond the level of local populations and therefore should belong to the same species.

Crossbreeding for valid species detection (sensu Mayr 1967)

Because of lack of confirmation in some genetic aspects (see above) crossbreeding experiments between all of the available Chilean populations (including the four dealt with here "species"; see fig.4: 1-7) were started some years ago. According to Mayr's concept of valid species ("biospecies concept"), hybrid fertility indicates that the tested forms will belong to the same species while hybrid sterility shows the borders between true or valid species. This statement concerning hybrid fertility is - as well known - regularly applied to hybrids which occur under natural conditions. However, cases as *Orestias* or as many other Old and New World oviparous cyprinodonts, which interspecifically do neither show ecological nor (courtship) behavioural differences under natural conditions, do not present considerable reasons for excluding their fertile "species" hybrids from Mayr's biospecies concept - only because they are products of controlled aquarium crossbreeding. This opinion is basically confirmed by the

comparison of identic results in histological gonad structures of F_1 -hybrids - natural vs. aquarium hatched ones - of two Mediterranean *Aphanius* species (cf. Villwock 1985, 1987). The above mentioned crossbreeding in Chilean *Orestias* resulted without any exception in fertile F_1 -hybrids, which led to numerous F_2 and already F_n offspring. This is one additional argument that the different Chilean *Orestias* populations belong to the same species, which is according to our suggestions *O. agassizii*.

Conclusions

The results of the various investigations that have been referred to above lead to the following conclusions:

- (1) Evidently all Chilean *Orestias* populations belong to one single species.
- (2) This species is presumed to be identical with *Orestias agassizii*, the most widely spread species within the distribution patterns of the genus *Orestias* and the one with the broadest ecological tolerance. This assumption is based on the high degree of similarity, or highly corresponding characters as illustrated in morphometric and meristic evaluations and is confirmed by results of genetic investigations. A similar interpretation has already been published by Mann (1954), and even Parenti (1984) ranks the Chilean "species" in an *Orestias agassizii* complex.
- (3) The assumption that the species belong solely to one single unit which is identical with *O. agassizii* is confirmed by aging the given geological facts concerning the development of the present water bodies inhabited by the Chilean *Orestias* populations concerned, including the distribution patterns of *Orestias agassizii*. Geographic distance and time since isolation of this tropical fish community agree with this concept.

Discussion remarks at the Symposium

Question: Have you any information on longtime population density under natural conditions?

Answer: No, no precise ones, however there is no indication that the population size will differ very much from year to year. The Chilean populations remain seemingly on a numerical high level (about thousands / population).

Question: Are there obvious differences between observations in nature vs. aquaria controlled strains concerning ontogenetic stages?

Answer: No, as far as we know.

References

- Ahlfeld, F. & L. Branisa (1960): Geología de Bolivia. – Instituto Boliviano del Petroleo, La Paz.
- Arratia, F.G. (1982): Peces del Altiplano de Chile. – pp. 93-133 in: El hombre y los ecosistemas de Montaña. (ed. UNESCO). – MAB 6. El ambiente natural y las poblaciones humanas de los Andes del Norte Grande de Chile (Arica, Lat. 18°28'S). Vol. I. La vegetación y los vertebrados inferiores de los pisos altitudinales entre Arica y el Lago Chungará. Santiago de Chile.
- Costa, W.J.E.M. (1997): Phylogeny and Classification of the Cyprinodontidae revisited (Teleostei: Cyprinodontiformes): Are Andean and Anatolian killifishes sister taxa? – J.Comp.Biol. 2(1): 1-16.

- Eschmeyer, W.N. (1998): Catalog of fishes. – <http://www.fishbase.org/> Eschmeyer.
- Foerster, W. & F. Anders (1977): Zytogenetischer Vergleich der Karyotypen verschiedener Rassen und Arten lebendgebährender Zahnkarpfen der Gattung *Xiphophorus*. – Zool. Anz. 198: 167-177.
- Francis, P. & S. Self (1987): Verheerende Flankenabbrüche an Vulkanen. – Spektrum Wiss. 8: 86-93.
- Gold, J.R., W.J. Karel & M.R. Strand (1980): Chromosome formulae of North American fishes. – Progr. Fish-Cult. 42: 10-23.
- Gyldenholm, A.O. & J.J. Scheel (1971): Chromosome number of fishes. – J. Fish Biol. 3: 479-486.
- Harmon, R.S., J. Davidson, G. Wörner, L. López-Escobar, H. Moreno, N.J. McMillan, D. Turner & C. Nye (1987): Geology, chronology, geochemistry, and isotope character of the Nevados des Payachata volcanic group, N-Chile. – Act. X. Congr. Geol. Argentino, Tucumán, Argentina 4: 344-345.
- Karbe, L. (1961): Cytologische Untersuchung der Sterilitätserscheinungen bei anatolischen Zahnkarpfen, ein Beitrag zum Speziationsproblem. – Mitt. Hamburg. Zool. Mus. Inst. 59: 73-104.
- Kött, A., R. Gaupp & G. Wörner (1995): Miocene to Recent history of the western Altiplano in northern Chile revealed by lacustrine sediments of the Lauca basin. – Geol. Rundschau 84: 770-780.
- Lauzanne, L. (1981): Description de trois *Orestias* nouveaux du Lac Titicaca, *O. ispi* n.sp., *O. forgeti* n.sp. et *O. tchernavini* n.sp. (Pisces, Cyprinodontidae). – Cybium, 3. Serie, 5, 3: 71-91.
- Lauzanne, L. (1982): Les *Orestias* (Pisces, Cyprinodontidae) du Petit lac Titicaca. – Rev. Hydrobiol. trop., Bondy 15(1): 39-70.
- Loubens, G. & J. Sarmiento (1985): Observations sur les poissons de la partie Bolivienne du lac Titicaca II. *Orestias agassii* Valenciennes, 1846 (Pisces, Cyprinodontidae). – Rev. Hydrobiol. trop., Bondy 18(2): 159-171.
- Lueken, W. (1962): Chromosomenzahl bei *Orestias*. – Mitt. Hamburg. zool. Mus. Inst. 60: 195-198.
- Lüssen, A. (1998): Vergleichende Untersuchung zur frühen Ontogenie neuweltlicher Zahnkarpfen der Gattung *Orestias* VAL., 1839 (Teleostei, Cyprinodontidae) unter besonderer Berücksichtigung der Schuppenanlagen. – Diplom-Arbeit, Fachbereich Biologie, Universität Hamburg: 51 pp.
- Makino, S. (1951): An atlas of the chromosome numbers in animals. 2. ed. – The Iowa State College Press. Ames, Iowa, 27.
- Mann, G. (1954): Vida de los Peces en aguas chilenas. – Universidad de Chile: 195 und 196.
- Mayr, E. (1967): Artbegriff and Evolution, Parey, Hamburg (1st ed.: 1963: "Animal species and Evolution", Harvard University Press, Cambridge, Mass.).
- Moon, H.P. (1939): III. The geology and physiography of the Altiplano of Peru and Bolivia. – Trans. Linn. Soc. London 1: 27-43.

- Müller, R. (1993): Kritische Anmerkungen zur Revision der Gattung *Orestias* (Pisces: Cyprinodontidae) durch Parenti aus dem Jahr 1984. – Zool. Jb., Abt. Anatom. Ontogen. Tiere. G. Fischer, Jena.
- Nei, M. (1972): Genetic distance between populations. – Am. Nat. 106: 283-290.
- Newell, N. (1949): Geology of lake Titicaca region, Peru and Bolivia. – Geol. Soc. Am., Memoir, 36: 10-104.
- Nogusa, S. (1960): A comparative study of the chromosomes in fishes with particular considerations on taxonomy and evolution. – Mem. Hyogo Univ. Agric. 3(1), Biol. Ser. 62 pp (app.).
- Parenti, L.R. (1984): A taxonomic revision of the Andean killifish genus *Orestias* (Cyprinodontiformes, Cyprinodontidae). – Bull. Am. Mus. Nat. Hist. 178: 110-214.
- Parker, A. & I. Kornfield (1995): Molecular perspective on evolution and zoogeography of Cyprinodontid killifishes (Teleostei; Atherinomorpha).- Copeia 1: 8-21.
- Pinto, C. & I. Vila (1987): Relaciones tróficas y caracteres morfofuncionales de *Orestias laucaensis* Arratia, 1982 (Pisces, Cyprinodontidae). – Ann. Mus. Hist. Nat. Valparaíso 18: 77-84.
- Rab, P., P. Roth & B. Mayr (1987): Karyotype study of eight species of European percid fishes (Pisces, Percidae). – Caryologia 40 (4): 307-318.
- Roberts, F.L. (1967): Chromosome cytology of the Osteichthyes. – Progr. Fish-Cult. 29: 75-83.
- Schwalb, A., S.J. Burns & K. Kelts (1999): Holocene environments from stable isotope stratigraphy of ostracods and authigenic carbonate in Chilean Altiplano lakes. – Palaeogeogr., Palaeoclimatol., Palaeoecol. 148: 153-168.
- Tchernavin, V. V. (1944): A revision of the subfamily Orestiinae. – Proc. Zool. Soc., London 114, 9: 140-233.
- Thomann, R. (1990): Systematische und ökologische Untersuchungen an *Orestias* – Populationen (Valenciennes, 1839) (Pisces: Cyprinodontidae) im chilenischen Hochland., Dissertationsschrift, Fachbereich Biologie der Universität Hamburg., 135 S.
- Uyeno, T. & R.R. Miller (1972): Second discovery of multiple sex chromosomes among fishes. – Experientia 28: 223-225.
- Uyeno, T., R.R. Miller & J.M. Fitzsimonis (1973): Karyology of the cyprinodontoid fishes of the Mexican family Goodeidae. – Copeia 2: 497-510.
- Vila, I. & M. Pinto (1986): A new species of killifish (Pisces, Cyprinodontidae) from the Chilean altiplano. – Rev. Hydrobiol. trop., Bondy 19(3-4): 233-239.
- Villwock, W. (1963): Genetische Analyse des Merkmals "Beschuppung" bei anatolischen Zahnkarpfen (Pisces, Cyprinodontidae) im Auflöserversuch. – Zool. Anz. 170 (1-2): 23-45.
- Villwock, W. (1966): Zur Biologie der Orestiinae (Pisces: Cyprinodontidae), unter besonderer Berücksichtigung von Darminhaltsuntersuchungen. Ein Beitrag zum Problem der Speziation in der Gattung *Orestias*. – Abh. Verh. nat.wiss. Ver. Hamburg, (NF) 10: 153-166.

- Villwock, W. (1985): Über Naturbastarde zwischen zwei validen Arten der Gattung *Aphanius* Nardo, 1827 (Pisces: Cyprinodontidae) aus der Bardawil-Lagune, Nordsinai/Ägypten. – Mitt. hamb. zool. Mus. Inst. 82: 311-317.
- Villwock, W. (1987): Further contributions on natural hybrids between two valid species of *Aphanius*, *Aphanius dispar dispar* (Rüppell) and *Aphanius fasciatus* (Valenciennes) (Pisces, Cyprinodontidae) from the Bardawil-Lagoon, North Sinai and Al-Qanatir, west of the Suez Canal, Egypt. – pp. 238-244 in: Proc. Symp. Fauna and Zoogeogr. Middle East (eds. Krupp, F., W. Scheider & R. Kinzelbach). – Beih. Tübinger Atlas Vord. Orient, Reihe A (Naturwiss.) 28.
- Villwock, W. & U. Sienknecht (1993): Die Zahnkarpfen der Gattung *Orestias* (Valenciennes, 1839) (Teleostei: Cyprinodontidae) aus dem Altiplano von Bolivien, Chile und Peru. Ein Beitrag zur Entstehung ihrer Formenvielfalt und intragenerischen Verwandtschaftsbeziehungen. – Mitt. hamburg. zool. Mus. Inst. 90: 321-362.
- Villwock, W. & U. Sienknecht (1995): Intraspezifische Variabilität im Genus *Orestias* Valenciennes, 1839 (Teleostei: Cyprinodontidae) und zum Problem der Artidentität. – Mitt. hamburg. zool. Mus. Inst. 92: 381-398.
- Villwock, W. & U. Sienknecht (1996): Contribución al Conocimiento e Historia de los Peces Chilenos. Los Cyprinodóntidos del Género *Orestias* Val., 1839 (Teleostei: Cyprinodontidae) del Altiplano Chileno. – Medio Ambiente, Ambiente Acuáticos 13 (1): 119-126.
- Villwock, W. & R. Thomann (1987): Mitteilung über einen neuen Fundort von *Orestias* (Valenciennes, 1839) (Pisces: Cyprinodontidae) aus dem nördlichen Altiplano von Chile. Ein Beitrag zur Kenntnis der Verbreitung der Gattung *Orestias*. – Mitt. hamburg. zool. Mus. Inst. 84: 167-174.
- Villwock, W., L. Kies, F. Thiedig & R. Thomann (1987): Geologisch-ökologische Untersuchungen am Lago Chungará/ Nord Chile: Zielsetzungen und erste Ergebnisse (Investigaciones geológicas y ecológicas en el Lago Chungará/ norte de Chile: Objetivos y primeros resultados). – IDESIA (Chile) 9: 21-34.
- Vitturi, R., E. Catalano, M.S. Colomba, L. Montagniao & L. Pellerito (1995): Karyotype analysis of *Aphanius fasciatus* (Pisces, Cyprinodontiformes): Ag-NORs and C-band polymorphism in four populations from Sicily. – Biol. Zentr.bl. 114: 392-400.
- Vitturi, R., A. Libertini, A. Mazzola, M.S. Colomba & G. Sara (1996): Characterization of mitotic chromosomes of four species of the genus *Diplodus*: Karyotypes and chromosomal nuclear organizer region phenotypes. – J. Fish Biol. 49: 1128-1137.
- Wörner, G., R.S. Harmon, J. Davidson, S. Moorbath, D.L. Turner, N. McMillan, C. Nye, L. Lopez-Escobar & H. Moreno (1988): The Nevados de Payachata volcanic region (18°S/69°W, N. Chile). I. Geological, geochemical and isotopic observations.- Bull. Volcanol. 50: 287-303.
- Zeil, W. (1979): The Andes. A geological review. – In: Beiträge zur regionalen Geologie der Erde (eds. Bender F., V. Jacobshagen et al.). – Gebrüder Borntraeger, Berlin, Stuttgart.

Zeil, W. (1984): Die Salare in Nordchile – Geologie, Struktur und Geochemie.–
Geotekton. Forsch. 67(I-II): 1-146.

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Diversity of a snake community in a Guinean rain forest (Reptilia, Serpentes)

Wolfgang Böhme

Abstract: During a one month excursion to the Zيام Forest (Forêt de Zيام), SE Guinea, a total of 38 species of snakes was collected, 5 of them being new for the fauna of Guinea. The only two earlier herpetological or ophidiological expeditions in this area (see Chabanaud 1920/21, Condamin 1959) recorded 24 snake species. Of these, 4 were not present in my collection, so that a total of 42 species is known from this small part of the West African rain forest, which approaches the published record (45: see Trape 1985) of any African snake assemblage. The species accumulation curve even suggests a much higher species richness in this forest.

Whereas the anuran fauna in the same area was also comparatively rich (29 species recorded in one month), the lizard assemblage proved to be less rich (11 species only). An evaluation of the food niches of the 38 syntopic snake species encountered demonstrates a correspondingly low number of lizard-eaters (which are predominant in savannas), but many forms specializing in small mammals, birds, frogs and fish, some even in other snakes (*Mehelya*) and arthropods (*Aparallactus*).

Key words: Reptilia, Serpentes, species richness, abundance, niche segregation, SE Guinea, West Africa

Introduction

On behalf of the PROGERFOR (Forest Gestation Resource Project, Ministry of Agriculture and Animal Resources at Conakry, Republic of Guinea), I spent the entire month of October 1993 in this West African country. PROGERFOR has a strong nature conservation component and tries to withhold the major part of two large and relatively intact forests from exploitation by forestry management. These forests are (1) the Zيام Forest (Forêt de Zيام) of approx. 1300 km², and (2) the Diécké Forest (Forêt de Diécké) of about 700 km², both situated in the extreme SE of the country where it meets, in the triangle between Liberia and Ivory Coast, the northern margin of the West African (= Upper Guinean) rain forest block (fig. 1).

My efforts to survey the herpetofauna of the two forests to be protected, within the framework of other zoological and botanical inventories of both forests, were concentrated on the Zيام Forest, and I was based in the PROGERFOR compound at Sérédou, hosted by the head of this project, Prof. Dr. Wilfried Bützler. In contrast to the Diécké Forest, which occupies a rather flat area as a lowland forest, the Zيام Forest covers a hilly area with steep slopes, fast-running torrents and waterfalls reaching up to 1400 m a.s.l., but also has more level areas with slow-running forest rivers and creeks. Primary forest is still extant on the slopes, and also in the level areas, and where it has

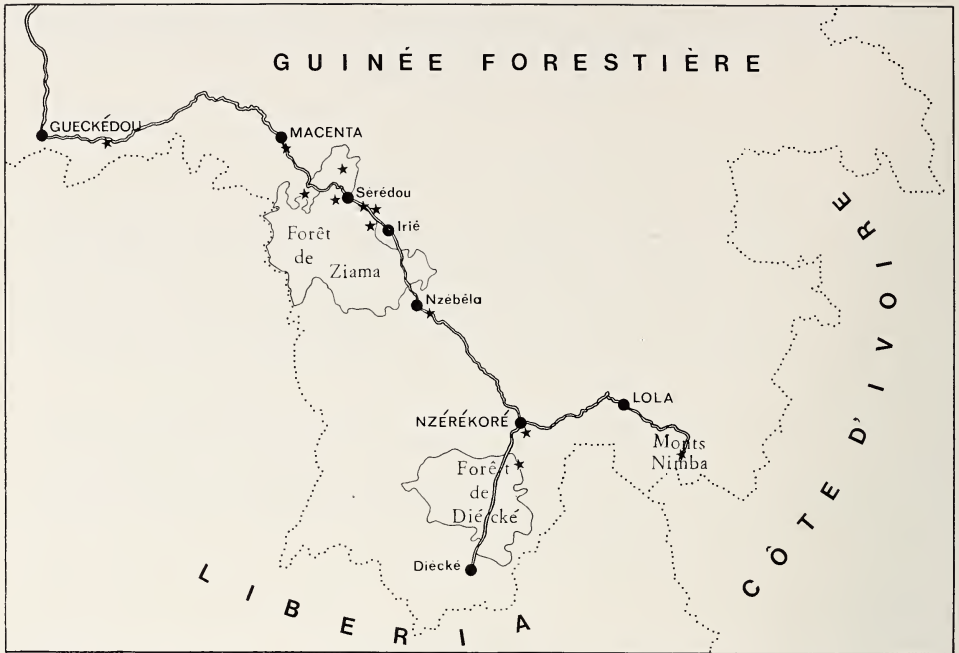


Fig.1: Map of SE Guinea with the Ziam and Diéké forests. Stars indicate collection sites.

been (illegally) destroyed (including deforestation by fire) it is reforested with local timber such as *Terminalia*. From 1300-1400 m a.s.l. the vegetation already contains montane floral elements, e.g. the widely distributed African tree fern *Cyathea manniana*. For a detailed description of habitats, see Böhme (1993, 1994 and in prep.).

Material and methods

Of the four weeks I spent in Guinea, I was actually present for 20 days in the study area. During this period, a total of 81 amphibian and reptile species was collected: 1 caecilian, 29 anuran, 11 lizard and 40 snake species. Of these, 38 snake species were recorded only in the Ziam Forest, a total of 154 specimens, which are deposited in the ZFMK collection, Bonn.

Due to the limited time available, we tried to be as effective as possible and included the local people in our efforts. Moreover, we left buckets with preservative fluid in some villages which we controlled repeatedly. Some specimens included in the analysis were collected by Wilfried Bützler before and also after my visit, and a few other specimens, left for deposition in the teaching collection of the "Centre de Recherches" at Sérédou, are not included in the present analysis. In Bonn, the snake material was checked with regard to the stomach contents. Aspects of faunistic, morphological, systematic, and zoogeographical importance will be published elsewhere, together with information on the remaining herpetofauna obtained.

Table 1: The snake fauna of SE Guinea as documented by various authors

	Forêt de Ziamá, between Macenta and N'Zébéla			Forêt de Diécké, between N'Zérékoré and Diécké			Mt. Nimba region
Reference	Chabanaud (1920/21)	Condamin (1959)	Böhme (this paper)	Chabanaud (1920/21)	Angel et al. (1954)	Böhme (this paper)	Angel et al. (1954)
Family							
Subfamily							
Species							
Typhlopidae							
<i>Typhlops angeli</i>							+
<i>Typhlops punctatus liberiensis</i>		+	+	+		+	+
Boidae							
<i>Calabaria reinhardti</i>			+			+	
<i>Python sebae</i>	+						
Colubridae							
Colubrinae							
<i>Bothrophthalmus lineatus</i>		+	+	+		+	+
<i>Chamaelycus fasciatus</i>				+			+
<i>Gastrophys x smaragdina</i>	+	+	+	+			+
<i>Hapsidophrys lineatus</i>	+		+	+			+
<i>Lamprophis lineatus</i>				+			+
<i>Lamprophis olivaceus</i>		+	+	+			+
<i>Lamprophis virgatus</i>	+	+	+	+			+
<i>Gonionotophis klingi</i>							+
<i>Lycophidion irroratum</i>							+
<i>Lycophidion semicinctum</i>							+
<i>Homonotus modestus</i>							+
<i>Mehelya guirali</i>			+				
<i>Mehelya poensis</i>	+		+				+
<i>Mehelya stenophthalmus</i>			+				+
<i>Philothamnus carinatus</i>			+				
<i>Philothamnus heterodermus</i>	+		+				+
<i>Philothamnus irregularis</i>							+
<i>Philothamnus semivariegatus</i>		+					
<i>Meizodon coronatus</i>		+				+	+
<i>Meizodon regularis</i>			+				
<i>Thrasops occidentalis</i>			+				
Natricinae							
<i>Afronatrix anoscopus</i>	+	+	+	+	+	+	+
<i>Grayia smithii</i>	+	+	+	+			+
<i>Natriciteres variegatus</i>	+	+	+	+		+	+
Boiginae							
<i>Crotaphopeltis hotamboeia</i>	+	+	+	+			
<i>Dipsadoboa brevirostris</i>			+	+			+
<i>Dipsadoboa elongata</i>							+
<i>Dipsadoboa unicolor</i>	+		+	+			+
<i>Dispholidus typus</i>	+						
<i>Polemon acanthias</i>		+	+				+
<i>Polemon bocourti</i>							+
<i>Thelotornis kirtlandii</i>							+
<i>Psammophis phillipsi</i>	+	+	+	+		+	+
<i>Toxicodryas blandingii</i>	+	+	+	+			+
<i>Toxicodryas pulverulenta</i>	+		+		+		+
Dasypeltinae							
<i>Dasypeltis fasciata</i>			+				
<i>Dasypeltis scabra</i>							+

	Forêt de Zياما, between Macenta and N'Zébéla			Forêt de Diécké, between N'Zérékoré and Diécké					Mt. Nimba region
Family Subfamily Species	Reference Chabanaud (1920/21)	Condamin (1959)	Böhme (this paper)	Chabanaud (1920/21)	Angel et al. (1954)	Roman (1976)	Wallach (1994)	Böhme (this paper)	Angel et al. (1954)
Atractaspididae									
<i>Aparallactus lineatus</i>			+				+		+
<i>Aparallactus modestus</i>		+	+						+
<i>Aparallactus niger</i>		+	+	+			+		+
<i>Atractaspis irregularis</i>		+	+						+
Elapidae									
<i>Dendroaspis viridis</i>	+	+	+	+	+				+
<i>Naja melanoleuca</i>	+	+	+	+	+				+
<i>Naja nigricollis</i>		+	+						+
<i>Pseudohaje nigra</i>						+		+	
Viperidae									
Causinae									
<i>Causus lichtensteini</i>		+			+				
<i>Causus maculatus</i>	+	+	+	+				+	+
Viperinae									
<i>Atheris chlorechis</i>	+	+	+						+
<i>Bitis gabonica</i>	+	+	+	+				+	+
<i>Bitis nasicornis</i>	+	+	+	+				+	+

Results and discussion

Species richness: The herpetofauna of Guinea is extremely poorly known (see Böhme 1993, 1994 and in prep. for a detailed historical overview). For the study area dealt with here, this poor knowledge is illustrated by the following facts:

1. I was the first person to search for amphibians and reptiles in this area (since 1959 in the entire country!) since 1958, when Mr. R. Pujol finished a 5-month expedition at Sérédou (Condamin 1959). Of the 24 snake species collected by R. Pujol, 4 were not represented in my collection, resulting in a total number of 42 species for the Zياما Forest snake assemblage!

2. No less than 5 species collected during my visit have not been recorded for Guinea before. They are: *Calabaria reinhardti*, *Meizodon regularis*, *Thrasops occidentalis*, *Mehelya guirali*, and *Dasypeltis fasciata* (for details see Böhme, 1993, 1994 and in prep.).

3. Several of the remaining species collected by us were known in Guinea only from Mt. Nimba, to which the French herpetological activities in Guinea were restricted. They made Mt. Nimba famous as a center of endemism, mainly because it was the only site where data were available. The inclusion of the Zياما and Diécké Forests into herpetological surveying demonstrated that nearly all Mt. Nimba snakes also occur elsewhere.

The information summarized above is documented in more detail in table 1.

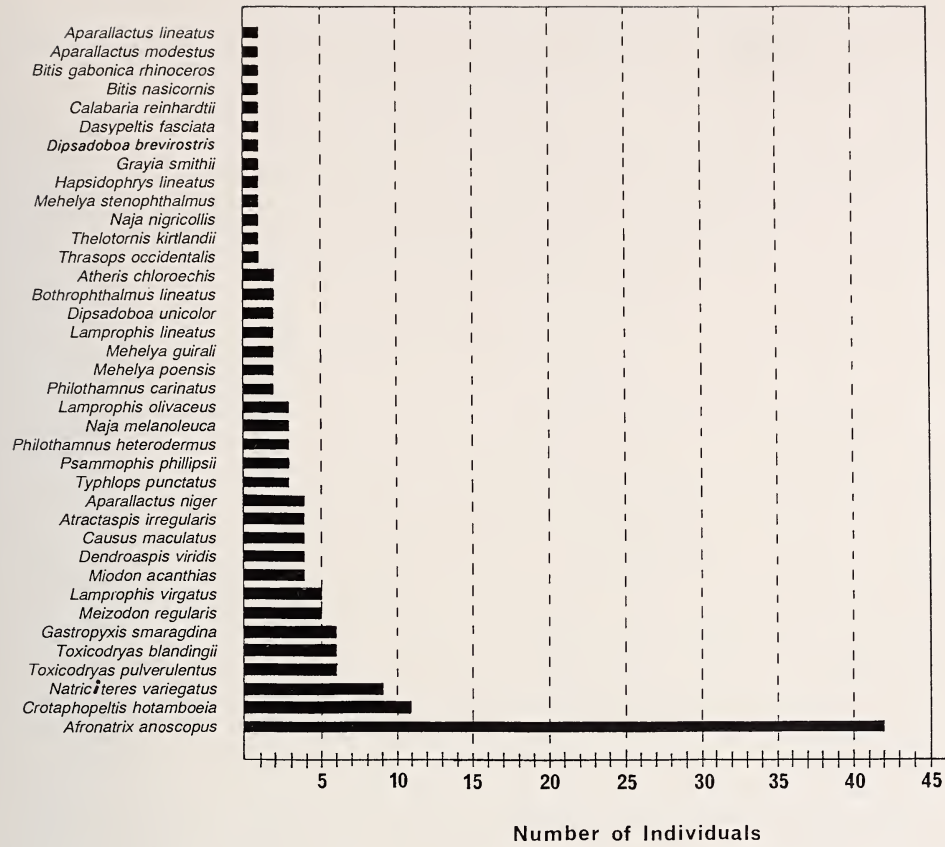


Fig.2: Species richness and abundance in the Ziama Forest snake community.

Abundance: Fig.2 combines the species richness with the abundance data in order to give an idea of the diversity of this snake community. By far the most dominant species (during October 1993) was *Afronatrix anoscopus*. Of 154 specimens in total, 42 belonged to this aquatic species, which is 27.3 % of the entire community. Together

Activity Micro-habitat			predominantly	
			diurnal	nocturnal
			18	17
predominantly	terrestrial	19	7	12
	aquatic	4	4	—
	arboreal	12	7	5
	fossorial	7	7	

Fig.3: Species and niche occupation of the Ziama Forest snake community. Some species may appear twice as they can be diurnal and nocturnal as well as semiterrestrial, -aquatic, and -arboreal

Table 2: Ecological classification of the Zيام Forest snake community; n - nocturnal; d - diurnal; aq - aquatic; ar - arboreal; f - fossorial; t - terrestrial. For the numbers of food categories see text.

Snake species	Activity & Microhabitat	Food categories
<i>Aparallactus lineatus</i>	n f/t	7/ 6
<i>Aparallactus modestus</i>	n f/t	7b/ 6a
<i>Bitis gabonica rhinoceros</i>	n t	1a, c/ 2a/ 4a
<i>Bitis nasicornis</i>	n t	1a/ 4a/ 5/ -2a
<i>Calabaria reinhardtii</i>	n f	1a/ 7/ 8a
<i>Dasyeltis fasciata</i>	n t	2b
<i>Dipsadoboa guineensis</i>	n ar	4a/ ?
<i>Grayia smithii</i>	d aq	5/ 4a
<i>Hapsidophrys lineatus</i>	d ar	3a/ 4a
<i>Mehelya stenophthalmus</i>	n t	3a,b,c/ 4a
<i>Naja nigricollis</i>	d t	1a/ 2a,b/ 3a,b,c/ 4a/ 6a/ -7/ -8
<i>Thelotornis kirtlandii</i>	d ar	3a,c/ 2a,b/ 4a/ 6a
<i>Thrasops occidentalis</i>	d ar	2a/ 3a/ 4a
<i>Atheris chlorechis</i>	n ar	3a/ 1a
<i>Bothrophthalmus lineatus</i>	n t	1a
<i>Dipsadoboa unicolor</i>	n ar	4a
<i>Lamprophis lineatus</i>	n t	1a/ 2a,b/ 3a,b,c/ 4a
<i>Mehelya guirali</i>	n t	3c/ 3a/ 4a
<i>Mehelya poensis</i>	n t	3a,b,c/ 4a
<i>Philothamnus carinatus</i>	d t/ar	4a
<i>Lamprophis olivaceus</i>	n t	1a/ 3a
<i>Naja melanoleuca</i>	n/d t	1a/ 4a/ 3a,b,c/ 5/ 2a,b
<i>Philothamnus heterodermus</i>	d ar	4a/ 3a
<i>Psammophis phillipsii</i>	d t	1a/ 3a/ 4a/ 2a
<i>Typhlops punctatus</i>	n f	6a,b/ 8a
<i>Aparallactus niger</i>	n f/t	7/ 6
<i>Atractaspis irregularis</i>	n f	1a/ 3c
<i>Causus maculatus</i>	d t/aq	4a
<i>Dendroaspis viridis</i>	d t/ar	1a/ 2a
<i>Miodon acanthias</i>	n f/t	3b,c/ 4b
<i>Lamprophis virgatus</i>	n t	1a/ 3a/ 4a
<i>Meizodon regularis</i>	d t	1a
<i>Gastropyxis smaragdina</i>	d t	3a/ 4a
<i>Toxicodryas blandingii</i>	n ar	2a,b/ 3a/ 1b/ -4a
<i>Toxicodryas pulverulentus</i>	n ar	1a/ 2a/ 3a
<i>Natriciteres variegatus</i>	d aq	4a/ 5/ 7c
<i>Crotaphopeltis hotamboeia</i>	n t	4a/ 3a/ 1a
<i>Afronatrix anoscopus</i>	d aq	5/ 4a

with the next five commonest species - 11 *Crotaphopeltis hotamboeia*, 9 *Natriciteres variegatus*, 6 *Toxicodryas pulverulentus*, 6 *Toxicodryas blandingii*, and 6 *Gastropyxis smaragdina* - already more than 50 % (viz. 51,8 %) are represented. The remaining 32 species, represented by five to one specimens each, form roughly the second half of the community.

Spatial and temporal niche segregation: In table 2, an ecological classification is given for the spatial (terrestrial, fossorial, aquatic, arboreal) and temporal (diurnal, nocturnal) niche occupation of the snake assemblage. Fig.3 summarizes the result: The dominant species are either aquatic or terrestrial, with the exception of the terrestrial *Crotaphopeltis hotamboeia*. The sum resulting from the figure exceeds the 38 species studied as some of them can show up in more than one category, as they may be diurnal

and nocturnal, or terrestrial **and** aquatic, terrestrial **and** arboreal etc. (see table 2). Fossorial snakes are of course not differentiated in diurnal vs. nocturnal forms. The lack of nocturnal, aquatic snakes is remarkable, which could be expected as an antipredator strategy of ectothermic reptiles which, however, might be unable to compensate nocturnal temperature loss in an aquatic environment.

Trophic niche: The trophic niche is correlated with the habitat. Birds are mostly preyed upon by arboreal forms, whereas the aquatic forms prey predominantly on fish and frogs. The species of the Ziama snake community were classified as to their main prey types. These were divided in the following categories:

- | | |
|---------------------------------------|------------------------|
| 1. Mammals | 5. Fishes |
| a - small mammals: shrews, rodents | |
| b - bats | |
| c - larger mammals | |
| 2. Birds | 6. Insects |
| a - adults and nestlings | a - imaginal stages |
| b - eggs | b - larval stages |
| 3. Reptiles | 7. Other arthropods |
| a - lizards with well developed limbs | a - millipedes |
| b - serpentiform lizards | b - centipedes |
| c - snakes | c - spiders |
| 4. Amphibians | 8. Other invertebrates |
| a - anurans | a - worms |
| b - caecilians | b - molluscs |

The assignment of the snakes to these prey categories is also summarized in table 2. This is based on my own data, supplemented with information from Pitman (1974), Leston & Hughes (1968), Stucki-Stirn (1979) and Broadley (1983). Euryphagous species can easily be differentiated from stenophagous ones.

A striking phenomenon is the poor lizard assemblage of the Ziama Forest with only 11 species encountered. Whether this is a collecting artefact or the real species richness (or rather "poorness"!) might also be reflected by the number of lizard-eating (prey type 3 b) snake species. Out of 38 species, they are only 17 in number, most of them not narrowly specialized in this kind of prey. This suggests that lizards do not play a comparable role as snake prey in this forest community as they do in savanna reptile communities. The great trophic diversity of this species-rich snake community is, apart from rodent-, bird-, lizard-, frog-, fish-, and even arthropod-eaters, best demonstrated by the extreme specialists such as *Mehelya*, feeding to a great extent on other snakes, and *Dasypeltis*, feeding only on bird' eggs: a unique specialization lacking in the Amazonian and Malayan tropics.

Comparison with other snake communities: Species richness data for African snake communities have been compiled by Trape (1985). Four assemblages from Ivory Coast, Ghana, Gaboon, and CAR each ranged between 35 and 39 species. He himself recorded 45 species (represented by 351 specimens) at the forest site Dinamika (People's Democratic Republic of Congo = Congo-Brazzaville), which is still the published continental African record. The Ziama assemblage approaches this record.

A recent inventory of the snakes of the Comoe National Park (Ivory Coast) (Rödel et al. 1995) revealed 37 species collected over a period of 4 years. Rödel et al. (in press) were able to add 7 more species, resulting in a total of 44 species in this area. Their suspicion that up to 25 further snake species remain to be discovered in Comoe NP leads to a new quality of African snake species richness. There is, however, already evidence that such numbers are actually reached by some snake communities in Cameroon (C. Wild, pers. comm.)!

There are, however, some serious problems in comparing these data. The most important are (1) varying sizes, reliefs and habitat structures of the respective areas; and (2) varying collecting effort (so-called "man-days" *sensu* Murphy et al. 1994). This is the more true for snake diversity data from other places in the tropics. Neotropical forest snake communities from comparable areas vary between 36 (Arima Valley, Trinidad) and 60 species (Chagres, Panama), whereas Malayan richness data are available for a Bornean (36) and a Thai (47) forest site (Dunn 1949, Inger & Colwell 1977, Murphy et al. 1994).

In the Bornean study area (Danum Valley: Murphy et al. 1994), 161 snakes - representing 36 species - were collected in 166 days. This means 0.9 snakes per day. The Guinean study area (Forêt de Ziama) revealed similar numbers of specimens and species, viz. 154 snakes representing 38 species a considerably shorter time, but also with a differing number of collectors. In any case, considering the fact that in both cases formerly uncollected species were found even on the very last day of the field-trip (see fig.4), the total of 42 snake species recorded for the Ziama forest snake community

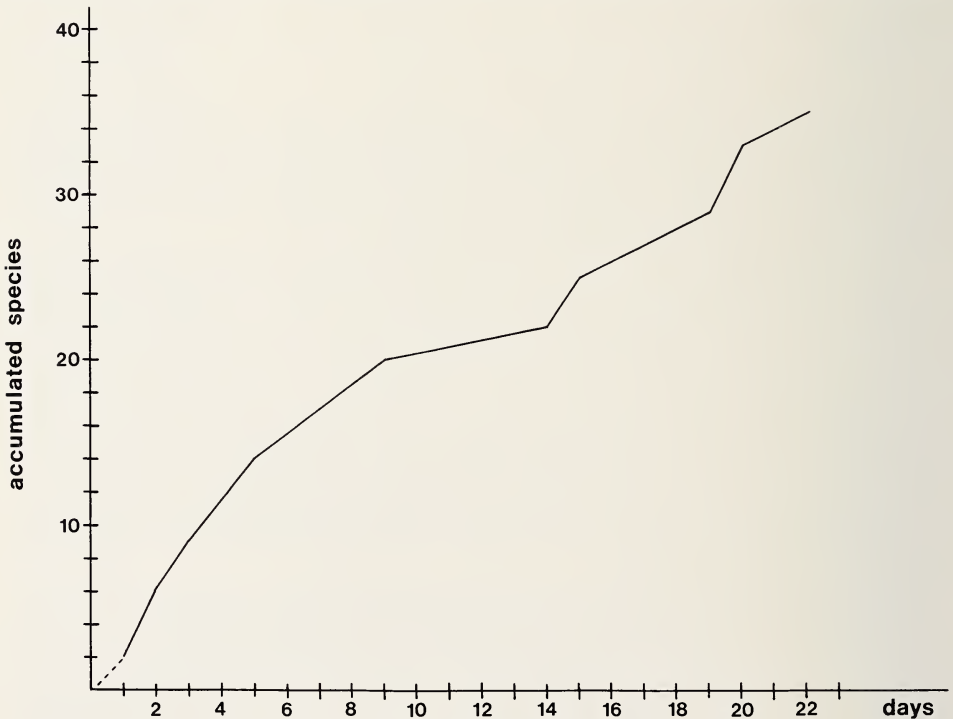


Fig. 4. Species accumulation curve of the Ziama Forest snake community

in SE Guinea is very likely to be much exceeded when more time is available for future investigations.

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References

- Angel, F., J. Guibé, M. Lamotte & R. Roy (1954): La Réserve Naturelle Intégrale du Mont Nimba. Serpents. – Mém. Inst. fr. Afr. Noire, Dakar, 40 (2): 381-402.
- Böhme, W. (1993): Mission d'études herpétologiques dans les forêts de Ziam et Diécké, Guinée forestière. – Unpubl. project report, Neu-Isenburg (DFC), 49 pp.
- Böhme, W. (1994): Frösche und Skinke aus dem Regenwaldgebiet Südost-Guineas, Westafrika. I and II. – Herpetofauna, Weinstadt, 16 (92): 11-19, and 16 (93): 6-16.
- Broadley, D.G. (1983): Fitzsimons' snakes of southern Africa. – Delta Books, Johannesburg.
- Chabanaud, P. (1920): Contribution à l'étude de la faune herpétologique de l'Afrique occidentale. Note préliminaire sur les résultats d'une mission scientifique en Guinée française (1919-1920). – Bull. Com. Étud. Hist. Sci. Afr. Occ. Fr., Paris, 1920: 489-497.
- Chabanaud, P. (1921): Contribution à l'étude de la faune herpétologique de l'Afrique Occidentale. Deuxième note. – Bull. Com. Étud. Hist. Sci. Afr. Occ. Fr., Paris, 1921: 445-472.
- Condamine, M. (1959): Serpents récoltés à Sérédou (Guinée) par R. Pujol. – Bull. Inst. Fr. Afr. Noire, Dakar, 21 (A 4): 1351-1366.
- Dunn, E.R. (1949): Relative abundance of some Panamanian snakes. – Ecology, 39 (1): 39-57.
- Inger, R.F. & R.K. Colwell (1977): Organisation of contiguous communities of amphibians and reptiles in Thailand. – Ecol. Monogr., 47: 229-253.
- Leston, D. & B. Hughes (1968): The snakes of Tafo, a forest cocoa-farm locality in Ghana. – Bull. Inst. Fond. Afr. Noire, Dakar, 30 (A2): 737-770.
- Murphy, J.C., H.K. Voris & D. Karns (1994): A field guide and key to the snakes of the Danum Valley, a Bornean tropical forest ecosystem. – Bull. Chicago Herpetol. Soc., 29 (7): 133-151.
- Pitman, C.R.S. (1974): A guide to the snakes of Uganda. Revised edition. – Wheldon & Wesley, Codicote, 290 pp.

- Rödel, M.-O., K. Grabow, C. Böckheler & D. Mahsberg (1995): Die Schlangen des Comoé-Nationalparks, Elfenbeinküste (Reptilia: Squamata: Serpentes). – Stuttg. Beitr. Naturk., (A) 528: 1-18.
- Rödel, M.-O., K. Kouadio & D. Mahsberg (1999): Die Schlangenfauna des Comoé-Nationalparks, Elfenbeinküste: Ergänzungen und Ausblick. – Salamandra, Rheinbach, 35(3): 165-180.
- Roman, B. (1976): Serpents mortels de l'Ouest Africain. – Étud. Sci., Paris 6: 1-56.
- Stucki-Stirn, M.C. (1979): Snake report 721. A comparative study of the herpetological fauna of the former West Cameroon/Africa. – Herpeto-Verlag, Teuffenthal, 650 pp.
- Trape, J.F. (1985): Les serpents de la région de Dimonika (Mayombe, République Populaire du Congo). – Rev. Zool. Afr., Bruxelles 99: 135-140
- Wallach, V. (1994): *Aparallactus lineatus* (Peters) and *Aparallactus niger* Boulenger: two valid species from West Africa. – J. Herpetol. 28 (1): 95-99.

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The distribution of *Chromaphyosemion* Radda, 1971 (Teleostei: Cyprinodontiformes) on the coastal plains of West and Central Africa

Rainer Sonnenberg

Abstract: The species of the monophyletic genus *Chromaphyosemion* Radda, 1971 live in small streams and rivulets ('marigots') in the coastal plains from Togo to Gabon. In their distribution area, some glacial forest refuges are postulated, mainly in Cameroon, Equatorial Guinea and Gabon. It is assumed that evolution and biogeography of this genus is connected with the evolution of the Central African rainforest during the Quaternary. In this paper *Chromaphyosemion* is grouped into 16 forms, defined by their colour patterns. The distribution data show that the maximum diversity of this genus is found in the proposed glacial rainforest refuges of Cameroon, suggesting a structurally complex history of these old rainforest blocks.

Key words: Aplocheilidae, *Chromaphyosemion* biogeography, rainforest refuges

Introduction

Responsible for the biodiversity of African tropical ecosystems, according to some authors, is the influence of climatic changes during the Quaternary and the resulting fragmentation of rainforest (Maley 1991, Mayr & O'Hara 1986). This probably induced major extinctions and, as an effect of the fragmentation, an isolation of populations, genetic bottlenecks and later a recolonization, which affected rainforest-bound species especially (Huber 1998b). Of special interest are position and number of rainforest refuges. Some authors provide a map of various currently assumed refuges in Western and Central Africa (Hamilton & Taylor 1991, Lévêque 1997, Maley 1991, Sayer et al. 1992). In this paper I want to test if the distribution of a mainly rainforest-bound group of small aplocheilid fish with limited dispersal abilities correlates to these assumed refuges in their distribution area.

The recent distribution and evolution of aplocheilid species and species groups seems to be closely connected with the historical changes of rainforest distribution and climates through the Quaternary (Huber 1998b). This means that a detailed study of the phylobiogeography of these fish should give further insight into the history of the tropical rainforest in coastal lowlands. Especially the different forms of *Chromaphyosemion*, with their relatively small ranges, could contribute additional data to the studies of historical rainforest fragmentation.

The aplocheilid genus *Aphyosemion* Myers, 1924 is subdivided into several subgenera (Myers 1924, Huber 1977, Huber & Seegers 1977, Kottelat 1976, Radda 1971b, 1977). One of them, *Chromaphyosemion*, is clearly monophyletic (Amiet 1987, 1991, Seegers 1981) and here considered as a genus. *Chromaphyosemion* are

small fish which reach about 5-7 cm total length and live in small rivers and streams in the coastal lowlands from Togo to northern Gabon (Eberl 1996, Radda 1971a,b, 1975, Radda & Huber 1976, Radda & Pürzl 1977, 1987). They are isomorphic with marked sexual dimorphism. The different forms are commonly distinguished by male coloration and sometimes by female colour pattern as well. Scheel (1966, 1968, 1974, 1990) did much comprehensive work on this group, based on crossbreeding experiments and karyotyping of different populations. His results reveal a high degree of reproductive isolation and variable chromosome numbers between populations. At the beginning of his studies he synonymized all described species with *Aphyosemion bivittatum* (Lönnberg, 1895) which then was considered as a 'morphospecies' because no morphological character could be found to distinguish subunits, and colour patterns are not visible in preserved material (Scheel 1966, 1968: 166 ff.). Scheel himself was aware of the fact, that the BIV-group - as he named them after *A. bivittatum* - consists of different 'bio-species' (sensu Mayr). In 1974 and 1990 Scheel revalidated some of the 'species', which in his opinion also consist of groups of different 'bio-species'. Amiet (1987), Daget et al. (1986), Scheel (1968, 1990) and Seegers (1986) tried to clarify the taxonomic confusion in this group. Fish hobbyists as well tried to redefine the known species by their coloration (see Eberl 1996 for a comprehensive review, e.g. of Poliak and Legros).

According to the actual state of knowledge it is most practicable to treat the forms which can be separated by their colour pattern as species; this does not anticipate any other decision in the future. The aim of this study is a review of the distribution data of the different *Chromaphyosemion* species and the comparison of the results with the data on rainforest refuges in that area.

Material and Methods

Preserved specimens from the studied live populations and slides of their live coloration are stored in the collection of the 'Zoologisches Forschungsinstitut und Museum Alexander Koenig' (ZFMK). Additional distribution data and pictures are taken from Amiet (1987, 1991), Eberl (1996), Huber (1996), Langton (1996), Radda (1971a,b, 1975), Radda & Huber (1976), Radda & Pürzl (1977, 1981, 1982, 1987), Scheel (1966, 1968, 1974, 1990), Seegers (1997) and Teugels et al. (1992). Populations are grouped according to shared characters in body coloration and fin

Plate 3: A selection of forms (probably species) of *Chromaphyosemion* Radda. Figures 1-6 show forms, which are all named *C. splendopleure* by most authors, 7 *C. loennbergii* and 8 the population marked on the map with ?; Amiet refers this also to *C. loennbergii*.

1 (upper row, left) *C. splendopleure*, Tiko; 2 (upper row, right) *C. cf. splendopleure*, Muyuka, Police Station; 3 (second row, left; a.s.o.) *C. sp. aff. splendopleure* 'Dizangué', Mangoule; 4 *C. sp. aff. splendopleure* 'Kopongo', Kopongo CSK 95/27; 5 *C. sp. 07*, near Nkolbonda; 6 *C. sp.* 'Likado', Likado River; 7 *C. loennbergii*, Song Bibai; 8 *C. sp.*, Chutes d'Ekoum

Photographs by Eigelshofen (1,4,7, and 8) and Pohlmann (2,3,5, and 6)



colour patterns of adult males. The populations of one phenotype can be separated from other related phenotypes by one or more diagnostic characters or a combination of characters.

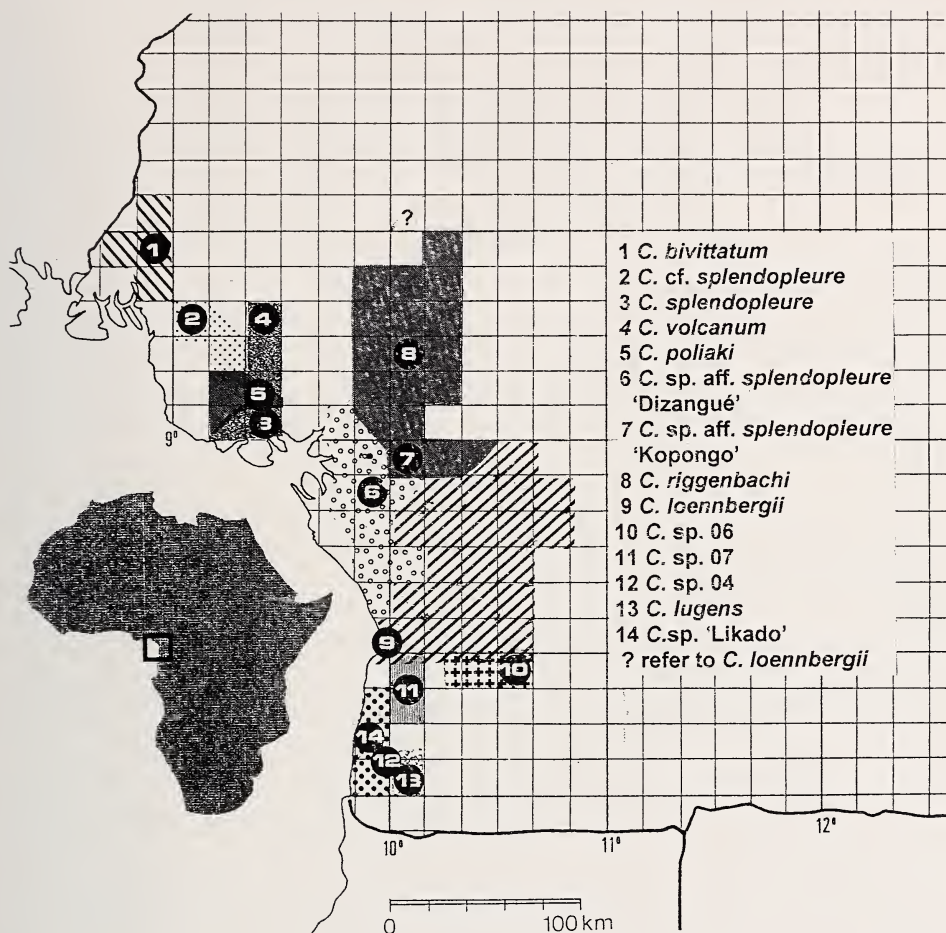


Fig.1: Map of the coastal plains of Cameroon with the schematic ranges of the *Chromaphysemon* species in Cameroon (modified after Amiet 1987). The numbers on the map correspond to the following species. If known, the number is placed at or near the terra typica.

Within the species accounts species names are used according to Daget et al. (1986) and Huber (1996) with addition of the species, described after the publication of these checklists. Here only those synonyms are given which occur in the literature used; additional synonyms are given in Daget et al. (1986), Seegers (1986) and Wildekamp (1993). Only a short description of the coloration is given, especially in those cases where I differ from previous authors; otherwise the first description is cited where a useful colour description is given. A more detailed description of body coloration and fin colour pattern of different species is given by Amiet (1987,

1991), who supplies a very detailed description for *Aphyosemion* s.l. along with a determination key, and Eberl (1996). For all species, the known distribution area and a reference to published pictures and / or preserved material is given. Poliak, Legros and Eberl (reviewed in Eberl 1996) separated populations of '*Aphyosemion splendopleure*' into three 'phenotypes', which are here redefined and in some aspects changed.

The distribution data of the species from Cameroon are presented in a map (fig.1). The pattern of species density and distribution is compared with published maps of postulated rainforest refuges in the area in question (Hamilton & Taylor 1991, Maley 1991, Sayer et al. 1992).

Results

Genus *Chromaphyosemion*

Chromaphyosemion Radda, 1971: 118 (type species: *Fundulopanchax multicolor* Meinken, 1930 by original designation). This name is considered to be a synonym of *Chromaphyosemion bitaeniatum* (Ahl, 1924) (see Seegers 1986). *Chromaphyosemion* was described by Radda (1971b) as a subgenus of *Aphyosemion*.

Diagnosis: *Chromaphyosemion* is distinct from all other *Aphyosemion* s.l. by two dark lateral bands in both sexes (vs. one or none). The male coloration can change very fast, depending on mood and hierarchical status of specimens (vs. less conspicuous changes in *Aphyosemion*). No blue or green metallic base colours on the sides of the body (vs. present in most other *Aphyosemion*). In males, two or three dorsolateral rows of scales with a metallic sheen (*C. riggenbachi* with none to two rows) (vs. no metallic sheen on these scales or a metallic sheen on the whole body). The form of unpaired fins in *Chromaphyosemion* is unique and differs from all species of *Aphyosemion* (Amiet 1987, Radda 1971b). Caudal fin rounded with pronounced dorsal and ventral streamers in males, sometimes trilobated in large specimens. Dorsal fin large and triangular. Anal fin trapezoid. In males, white, yellow or orange streamers are developed at unpaired fins, mostly with a different hue to that of the fins.

Amiet (1987), Huber (1996) and Scheel (1974) give the following additional combination of characters to define *Chromaphyosemion*: dorsal fin inserts above or slightly behind anal fin origin. Number of dorsal rays 9-14, number of anal rays 11-16, D/A- position 1/1-4 fin rays (vs. a higher number of anal and dorsal rays if the D/A-position is in the same range).

Amiet (1987), Murphy & Collier (1999) and Seegers (1981) showed that *Chromaphyosemion* is a monophyletic group with no apparent intermediate forms to *Aphyosemion* or related genera and therefore it is considered as a genus. The relationship to other species-groups remains unclear. A recent study on molecular systematics of *Aphyosemion* and *Fundulopanchax* fails to provide a well supported hypothesis – except the monophyly of most of the studied species groups (Murphy & Collier 1999).

Distribution: *Chromaphyosemion* species live in the coastal plains from Togo to northern Gabon. In the following species accounts the approximate distribution from West Africa to Central Africa is provided.

The species of *Chromaphyosemion*

Chromaphyosemion bitaeniatum (Ahl, 1924)

Terra typica: Niger, Nigeria

Synonyms: *Fundulus bitaeniatus* Ahl, 1924 - *Aphyosemion bitaeniatum* (Eberl 1996, Huber 1996, 1998a, Seegers 1986, 1997) - *Aphyosemion bivittatum* (Radda 1971b, Radda & Pürzl 1987, Scheel 1968, Schröder 1967) - *Aphyosemion multicolor* (Radda 1975, Radda & Pürzl 1981, Seegers 1981)

Examined material: ZFMK 21986 - 21987, Afanyangan (TMBB 90/13), Togo; ZFMK 21988 - 21989, Agbetiko (RT 97), Togo; ZFMK 21990 - 21991, Ibeju Creek, Nigeria; ZFMK 21992 - 21993, Yemoji River, Nigeria

Pictures: Eberl 1996 [p. 34, Lagos]; Radda & Pürzl 1987, [p.69, southern Benin]; Scheel 1968 [p. 116, Meko, Nigeria; p. 117, Umudike, Nigeria; p. 120 upper fig., Lagos, Nigeria]; Seegers 1997 [p. 59, fig. A03240-4 - A03244-4; p. 60, A03747-4 - A03749-4; p. 61, A03752-4]

Distribution: This species is found in the coastal plains from Togo to the Niger delta in Nigeria, which is about half of the distribution area of the genus. Along the Niger this species occurs further inland. From the eastern border of the distribution area one population is known from Umudike, which is between the river systems of the Niger and the Cross.

Remarks: Unpaired fins mainly orange with a blue or blue-green groundcolour. The amount of blue-green and orange in the anal fin can vary between and within different populations. A very conspicuous dark wound-like marking behind the operculum (Scheel 1974).

Scheel (1974) and Schröder (1967) showed that between different populations various degrees of reproductive isolation are found. Despite these findings there are only relatively small variations between the coloration of different populations.

Chromaphyosemion bivittatum (Lönnberg, 1895)

Terra typica: rivulet..., near the waterfall of river N'dian [Cameroon]

Synonyms: *Aphyosemion bivittatum* (Amiet 1987, Eberl 1996, Huber 1996, 1998a,b, Radda 1971a,b, 1975, Radda & Pürzl 1981, 1987, Radda & Wildekamp 1977, Scheel 1966, 1968, 1974, 1990, Seegers 1981, 1986, 1997)

Examined material: ZFMK 21994 - 21995, Kwa Riverfalls Plantation, Nigeria; ZFMK 21996 - 21997, Funge, Cameroon

Pictures: Amiet 1987 [plate 34, fig. 5-6]; Eberl 1996 [p. 22, Mundemba; p. 23, Funge and Biafra]; Radda & Pürzl 1987, [p.71, Funge]; Seegers 1997 [p. 61, A03245-4, A03246-4 and A03970-4]

Distribution: This species is known from the area between the Cross River (Nigeria) and Funge (Cameroon).

Remarks: *Chromaphyosemion bivittatum* is characterized by one, seldom two, dark spots on the base of the caudal fin in males (vs. absent in the closely related species *C. lugens* and *C. sp.* 06 (Amiet 1987, 1991, Eberl 1996)).

Chromaphyosemion cf. splendopleure (Brüning, 1929)

Synonyms: *Aphyosemion bivittatum* (Radda 1975, Scheel 1966, 1968) - *A. bitaeniatum* (Eberl 1996, in part) - *A. aff. multicolor* (Radda & Pürzl 1982, in part)

- *A. splendopleure* (Amiet 1987, Huber 1996, 1998a,b, Radda 1971a,b, Radda & Pürzl 1987, Scheel 1974, 1990, Seegers 1981, 1986, 1997, in part) - *A. splendopleure* 'Meme'-group (Eberl 1996, in part) - *A. sp. aff. splendopleure* (Radda & Wildekamp 1977)

Examined material: ZFMK 21998 - 21999, Lykoko, Cameroon; ZFMK 22000 - 22001, Muyuka Police Station (C 89/15), Cameroon

Pictures: Amiet 1987 [plate 37, fig. 16 and 19]; Eberl 1996 [p. 45, Muyuka Police Station]; Radda & Pürzl 1982, [p. 19, Oron, Nigeria], Radda & Pürzl 1987 [p. 70, Ekondo Titi, Cameroon]; Seegers 1981 [p. 156, fig. 6], Seegers 1997 [p. 122, A03530-4, A03945-4, A03947-4 only the right-hand picture; p. 123, A03948-4]

Distribution: These populations are found in the lower Cross in Nigeria (Radda 1975), and south of Funge to the Mungo River (Cameroon). Strains are known from Oron, Ekondo Titi, Mbonge, Lykoko, Owe and Muyuka.

Remarks: The colour of the unpaired fins is blue-green with yellow, the metallic sheen in the dorsal scales is yellow to gold and body colour can range from blue to pink, the throat and part of the belly are yellow. This separates *C. cf. splendopleure* from the nominate *C. splendopleure*. Eberl (1996) listed both forms under his 'Meme'-phenotype.

It is not known if the populations of the Cross River area are in connection with those of the Meme area or if they are divided by the distribution area of *C. bivittatum*. *C. cf. splendopleure* is closely related to *C. splendopleure*. It is possible that a cline between both species may be found in the area around Kumba, but in the area around Muyuka and Tiko they are easy to distinguish.

Chromaphysemon splendopleure (Brüning, 1929) and *C. volcanum* (Radda & Wildekamp, 1977)

Terra typica: Tiko in Kamerun [Tiko in Cameroon] (*C. splendopleure*) "...in einem kleinen Bächlein, welches durch den südwestlichen Stadtteil Kumbas fließt" [small rivulet, which flows through the southwestern part of Kumba = Kake River] (*C. volcanum*)

Synonyms: *A. splendopleure* (Amiet 1987, and Eberl 1996, in part) - *A. bivittatum* (Scheel 1968, in part) - *A. volcanum* (Amiet 1987, Eberl 1996, Huber 1996, Radda 1997, Radda & Pürzl 1987, Radda & Wildekamp 1977, Scheel 1990)

Examined material: ZFMK 22002 - 22003, Moliwe, Cameroon; ZFMK 22004 - 22005, Bamukong, Cameroon; ZFMK 22006 - 22007, Tiko, Cameroon; ZFMK 22008 - 22009, Bombe (CXC 23), Cameroon

Pictures: Amiet 1987 [plate 37, fig. 17-18]; Eberl 1996 [p. 52, *A. volcanum*]; Seegers 1997 [p. 122, A03946-4, A03949-4 and A03950-4]

Distribution: These species are known from Moliwe, Bamukong, Tiko, Yoke, Bombe and Kumba, which is an area from the foothills of Mount Cameroon to the region south of Lake Barombi Mbo. Most of the rivulets, in which this form is found, are tributaries of the River Mungo.

Remarks: These species have in general a red to orange body colour with a copper-red to reddish metallic sheen in the dorsal scales. Mainly orange-coloured unpaired fins with yellow to orange streamers. The throat is orange.

This group comprises two described species which are phenetically closer to each other than to the populations of *C. cf. splendopleure*. These species seem to be closely related compared with the following species, which are also included in *C. splendopleure* by various authors. *C. splendopleure* and *C. vulcanum* are here grouped together due to their apparent similarity and are treated as one group of closely related populations. There is an ongoing discussion in the aquaristic literature about the validity of the taxon *C. vulcanum* (e.g., Eberl 1996, Radda 1997) but neither reproductive isolation nor its reverse has been so far tested; herein both taxa are considered as valid until further data are provided.

Chromaphyosemion sp. aff. *splendopleure* (Brüning, 1929), 'Dizangué'

Synonyms: *Aphyosemion splendopleure* (Amiet 1987, Huber 1996, 1998a,b, Radda & Pürzl 1987, Scheel 1974, 1990, Seegers 1981, 1986, 1997, in part) - *A. splendopleure* 'Dizangué' (Eberl 1996) - *A. bivittatum* (Scheel 1968, in part)

Examined material: ZFMK 22010 - 22011, Mangoué, Cameroon

Pictures: Amiet 1987 [plate 36, fig. 13-14]; Eberl 1996 [p. 1, Dizangué]; Seegers 1997 [p. 122, A03943-4 and A03944-4]

Distribution: This species is found along the coast between Douala and Kribi. The western limit is the Atlantic Ocean and in the east it reaches the distribution areas of the species living further inland, *C. riggenbachi* and *C. loennbergii*.

Remarks: *C. sp. aff. splendopleure* ('Dizangué') differs from the nominate *C. splendopleure* in body coloration and fin colour pattern. The lower lateral band is characteristically very conspicuous. The dorsal part of the body is brown, below beige to green-yellow. The caudal fin has a mainly flame pattern but not on a blue groundcolour (like *C. loennbergii*). Together with the following species these fish show a marginal blue to blue-green band in the anal fin (vs. absence in the other two forms which were formerly included in *C. splendopleure*). The anal fin is in most populations translucent yellow-green (Amiet 1987) (vs. orange, orange-red or yellow in all other populations previously included in *C. splendopleure*). A wound-like marking as in *C. bitaeniatum* is present (vs. absence in the previous forms).

Chromaphyosemion sp. aff. *splendopleure* (Brüning, 1929), 'Kopongo'

Synonyms: *A. splendopleure* (Amiet 1987, Huber 1996, 1998a,b, Radda & Pürzl 1987, Scheel 1974, 1990, Seegers 1981, 1986, 1997, in part) - *A. splendopleure* 'Kopongo' (Eberl 1996) - *A. bivittatum* (Scheel 1968, in part)

Examined material: none

Pictures: Amiet 1987 [plate 36, fig. 15]; Eberl 1996 [p. 49, lower picture shows the Kopongo fish]

Distribution: This species is only known from a small number of localities around Kopongo (Amiet 1987, Eberl 1996). This area is possibly enclosed by the distribution of the 'Dizangué' species, but they are not in sympatry, or at the border of the *C. riggenbachi* area (see also Eberl 1996).

Remarks: *C. sp. aff. splendopleure* (Kopongo) differs from the previous species especially by fin coloration, and is possibly closer related to *C. loennbergii*. Only some red dots in the orange-coloured anal fin (vs. many in *C. loennbergii*). Anal fin

with a submarginal red and a marginal blue band (vs. absence of the blue band in *C. splendopleure* and *C. cf. splendopleure*). See Eberl (1996) for further details.

Chromaphyosemion poliaki (Amiet, 1991)

Terra typica: Cameroun: Province du Sud-Ouest:Tamben, [Cameroon: South west province: Tamben]

Synonyms: *Aphyosemion bivittatum* (Scheel 1968, in part) - *Aphyosemion poliaki* Amiet, 1991 (Eberl 1996, Huber 1996, 1998a,b, Seegers 1997) - *Aphyosemion volcanum* (Radda 1997, Radda & Pürzl 1987, in part)

Examined material: ZFMK 22012 - 22013, Ekona, Cameroon; ZFMK 22014 - 22015, Mile 29, Cameroon

Pictures: Amiet 1987 [plate 38, fig. 20-22], 1991 [p.90, 91]; Eberl 1996 [p. 55, Ekona; p. 56 Mile 29]; Radda & Pürzl 1987, [p. 72, Monea]; Seegers 1997 [p. 114, A03462-4 and A03463-4; p. 122, A03942-4]

Distribution: Only known from the southern and southeastern slopes of Mount Cameroon. In the coastal lowlands it is replaced by *C. splendopleure* and *C. cf. splendopleure*.

Remarks: Easy to distinguish from the surrounding populations of other species. Very dark fish with a brown body colour and very dark blue or violet to blackish unpaired fins. Sometimes up to four rows of metallic shining scales on the dorsal part of the sides. See Amiet (1991) for a detailed description.

Chromaphyosemion riggenbachi (Ahl, 1924)

Terra typica: Quelle bei Jahassi (Kamerun), [spring near Yabassi, Cameroon]

Synonyms: *Fundulus riggenbachi* Ahl, 1924 - *Aphyosemion riggenbachi* (Amiet 1987, Eberl 1996, Huber 1996, 1998a,b, Radda 1971a,b, Radda & Pürzl 1987, Scheel 1974, 1990, Seegers 1981, 1986, 1997) - *A. bivittatum* (Scheel 1968, in part)

Examined material: ZFMK 22016 - 22017, Nkwo, Cameroon; ZFMK 22018 - 22019, Cellucam (KEK 98/21), Cameroon

Pictures: Amiet 1987 [plate 33, Fig. 1-4]; Eberl 1996 [p. 27, C 89/19; p. 30, female C 89/23, male Nkapa; p. 33, HJRK 92/18 and C89/18]; Radda & Pürzl 1987 [p.73, near Yabassi, Cameroon]; Seegers 1997 [p. 117, A03482-4 and A03481-3]

Distribution: This species has one of the largest ranges. In the north it is limited by the foothills of the Bamileke Plateau. In the west it borders the area of the coastal forms between the Mungo and the Wouri. In the east the river Ouem and in the south the Sanaga are the assumed borders (Amiet 1987).

Remarks: Body coloration pale blue to blue-green, unpaired fins blue-grey to blue-yellow, streamers in most cases white or pale blue, in some populations yellow. The typical two lateral black bands are in most cases not seen in this species. It is the biggest species in this genus and can reach about 70 mm total length.

Chromaphyosemion loennbergii (Boulenger, 1903)

Terra typica: Kribi River [now Kienke River, Cameroon]

Synonyms: *Aphyosemion bivittatum* (Scheel 1968, in part) - *Aphyosemion loennbergii* (Amiet 1987, Eberl 1996, Huber 1996, 1998a,b, Legros 1999, Radda 1971a,b, Radda & Pürzl 1987, Scheel 1974, 1990, Seegers 1981, 1986, 1997)

Examined material: ZFMK 22020 - 22021, KEK 98/7, Cameroon

Pictures: Amiet 1987 [plate 34, fig. 7-8, plate 35, fig. 9-12]; Eberl 1996 [p. 40, Bipindi; p. 44 C 89/21, pair; p. 84 lower picture, Makondo]; Radda & Pürzl 1987 [p.74, near Kribi]; Seegers 1997 [p. 101, A03390-4 - A03394-4, A03901-4 - A03902-4]

Distribution: This species is found south of the Sanaga in the coastal plains. Its western limit seems to follow approximately the road from Edéa to Kribi. The Kienke River system seems to be the southern limit.

Remarks: *C. loennbergii* was collected syntopic with *C. sp. 06* on the road from Akom II to Bipindi. The caudal fin shows red flames on a blue groundcolour. The metallic sheen on the dorsolateral part of the body is golden to copper, throat can be blue or orange.

Amiet (1987) gives locality data of *C. loennbergii* north of the area of *C. riggenbachii*. Fish from one population (Chûtes d'Ekoum, see question mark on fig.1) were introduced to Europe in spring 1999. An F1 pair was examined in August. They differ from all known *C. loennbergii* populations, but further investigations are required.

Chromaphyosemion sp. 06

Synonyms: *Aphyosemion* aff. *lugens* (Vlaaming 1998)

Examined material: ZFMK 22022 - 22023 (KEK 98/9); ZFMK 22024 - 22025 (KEK 98/10)

Pictures: Vlaaming 1998, [p. 72, Mb607, ca. 25 km south of Bipindi, Cameroon]

Distribution: This fish was caught in 1997 by Vlaaming and 1998 by Eberl, Kämpf and Kliesch by the road between Akok and Akom and further north to Bipindi, where this species is syntopic with *C. loennbergii*.

Remarks: Together with *C. lugens* and *C. bivittatum* it forms a group of species with a very disjunct distribution. These three species are very similar in many unique aspects of coloration.

C. sp. 06 can be distinguished from *C. lugens* by the orange throat and the orange dorsal fin in both sexes (vs. absence in *C. lugens*). From *C. bivittatum* it can be distinguished by more regular lateral markings and the absence of the characteristic red dot at the base of the caudal fin.

Chromaphyosemion sp. 07

Synonyms: *Aphyosemion bivittatum* (Scheel 1968, 1990) - *A. loennbergii* (Radda 1971a, Scheel 1990, in part) - *A. sp. 07* (Legros 1999)

Examined material: ZFMK 22026 - 22027, KEK 98/6 (02°48'25"N, 10°02'10"E), Cameroon

Pictures: Scheel 1990 [p. 265, as *A. loennbergii*, Kribi, Cameroon; p. 373, as *A. bivittatum*, Lobe, Cameroon]

Distribution: Live specimens were caught in January 1998 by the road from Kribi to Ebolowa not far from Kribi. Pictures in Scheel (1990) show similar fish from the Kribi area. Further north it is replaced by *C. sp. aff. splendopleure* 'Dizangué' and in the south along the road to Campo by *C. sp.* 'Likado'. Further to the east only *C. loennbergii* and *C. sp. 06* are known.

Remarks: *C. sp. 07* differs from all other species in many coloration characteristics which are unique in their combination within *Chromaphyosemion*, possibly with the exception of *C. sp. 04*. The caudal fin shows red spots on a dark groundcolour (vs. flames in *C. loennbergii* (with blue groundcolour) and *C. sp. aff. splendopleure* 'Dizangué'). Adult specimens sometimes show a dark green coloration on the body (vs. light brown (beige) in *C. sp. aff. splendopleure* 'Dizangué' and orange to golden in *C. loennbergii*). The lower lateral black band can be very conspicuous while the upper band disappears (vs. both present or absent in all other species).

Chromaphyosemion lugens (Amiet, 1991)

Terra typica: Cameroun: Province du Littoral: Afan Essokié, [Afan Essokié, Cameroon]

Synonyms: *Aphyosemion lugens* Amiet, 1991 (Eberl 1996, Huber 1996, 1998a,b)

Examined material: ZFMK 22028 - 22029, near Afan Essokié (KEK 98/5), Cameroon

Pictures: Amiet 1991 [p.86, 87]; Eberl 1996 [p. 59 and p. 62, Afan Essokié]

Distribution: This species is only known from the Campo National Park around Afan Essokié (Terra typica) and the Massif des Mamelles, about 20 km to the north of there.

Remarks: *C. lugens* can be distinguished from its closest relatives *C. bivittatum* and *C. sp. 06* by the absence of orange colours on fins and body and the absence of the red dot at the base of the caudal fin which is characteristic of *C. bivittatum*.

Chromaphyosemion sp. 04

Synonyms: *A. splendopleure* (Seegers 1997, in part) - *A. sp. 04* (Eberl 1996, Legros 1999)

Examined material: ZFMK 22030 - 22031, Bibabivotou (HJRK 92/16), Cameroon

Pictures: Eberl 1996 [p. 71 and p. 81 upper picture]; Seegers 1997 [p.123, A03951-4]

Distribution: This species was caught near the village of Nazareth on the Bibabivotou river.

Remarks: In some characters *C. sp. 04* resembles *C. sp. 07* but before inclusion in this species further collections between the known localities are needed. This population does not show the dark green body colour. The dark lower lateral band is only seldom shown in dominant fish, as described for *C. sp. 07*. All unpaired fins

are identically coloured, except for a submarginal red and a marginal blue band in the caudal and anal fin. They show many red dots on a green-blue groundcolour (vs. different colour patterns between unpaired fins, flames or the absence of dots (mostly on the anal fin) in other species).

Chromaphyosemion sp. 'Likado'

Synonyms: *Aphyosemion splendopleure* (Brüning 1929), (Eberl 1996, Langton 1996, in part)

Examined material: ZFMK 22032 - 22033, Likado River, Cameroon,

Distribution: These fish were caught on the Likado River, along the road from Kribi to Campo. A similar population is known from Campo (Eberl 1996, Langton 1996).

Remarks: *C.* sp. 'Likado' shows a blue (Likado population) to green-blue (Campo population) colour on the dorsolateral part of the body which can change to brown in old individuals. Ventrally, the body is yellow to beige (vs. yellow only in the anterior part, or not yellow). The fins are yellow-green (Likado population) to green-blue (Campo population) with red dots.

Chromaphyosemion alpha (Huber, 1998)

Terra typica: PK 17,1 an der Straße vom Flugplatz Libreville (Hotel Gamba) zum Cap Estérias,....., nordwestliches Gabun [PK 17.1 by the road from the airport Libreville (Hotel Gamba) to Cap Estérias, northwestern Gabon]

Synonyms: *Aphyosemion splendopleure* (Huber, 1996, Radda & Huber 1976, Radda & Pürzl 1987, Seegers 1997, in part) - *Aphyosemion* sp. 02 (Eberl 1996) - *Aphyosemion alpha* Huber, 1998

Examined material: ZFMK 22034 - 22035, Cap Estérias (LEC 93/26), Gabon
Pictures: Eberl 1996 [p. 66 and 67, Cap Estérias]; Seegers 1997 [p. 123, A03952-3]; Huber 1998 [p. 17, 23]

Distribution: This species is only known from Cap Estérias, Gabon.

Remarks: *C. alpha* has a very unique coloration and at present no similar phenotype is known. For a detailed description of the coloration see Huber (1998a).

Chromaphyosemion kouamense (Legros, 1999)

Terra typica: 2,5 km nördlich von Nzog Bizeng (0°25'N, 10°04'E) [2,5 km north of Nzog Bizeng]

Synonyms: *Aphyosemion* aff. *loennbergii* (Huber 1998a) - *Aphyosemion kouamense* Legros, 1999 (Eigelshofen & Sonnenberg 1999) - *Aphyosemion* sp. 05 (Eberl 1996)

Examined material: ZFMK 22036 - 22037, Engong Kouame (LEC 93/24), Gabon

Pictures: Eberl, 1996 [p. 74, LEC 93/24; p. 77, PEG 94/ 48, LEC 93/24 female]; Legros, 1999 [p.35]

Distribution: This species is known only from localities on the road approximately between Mbèl Alen and Mveng Ayong at the foot of the Monts de Cristal.

Remarks: The specimens from the locality PEG 94/48 (near Mveng Ayong) differ in many aspects from the population of the type locality. Here we preliminarily follow the description and include them in this species. For a detailed description see Legros (1999), but note the remarks of Eigelshofen & Sonnenberg (1999).

Discussion

In this paper 16 forms are considered, many of them agree with already named taxa. *C. splendopleure* and *C. volcanum* are preliminarily treated as one species (but see under species accounts). The differences between them are considered to be an indication of a limited gene flow between these groups of populations, caused either by geographical or biological factors. A number of undescribed populations in Cameroon need further investigation before taxonomic conclusions can be drawn. The taxon *Chromaphyosemion splendopleure* is possibly a 'wastebin' of four species.

The species *C. pappenheimi* (Ahl, 1924) and *C. unistrigatum* (Ahl, 1935) are regarded as synonyms of *C. loennbergii* (Boulenger, 1903) (see Seegers 1986); however Scheel (1990) revalidated *C. pappenheimi*. It differs in coloration from *C. loennbergii* (Legros, pers. comm.; Scheel 1974), but there is no picture available for this population. Scheel's preserved material is deposited in Tervuren but could not be studied. Therefore in this paper *C. pappenheimi* is regarded as a synonym of *C. loennbergii*. This decision is supported by the fact that *C. pappenheimi* and *C. unistrigatum* are said to come from Bipindi (Ahl 1924, 1935), where today only *C. loennbergii* is found, whereas Scheel's population stems from a location east of Bipindi (Scheel 1974, 1990), so it is doubtful if this population represents one of the described species. The populations of Equatorial Guinea and Isla de Bioko are not included in this study because the only available data are given by Roman (1971), Scheel (1972, 1974) and Thys van den Audenaerde (1967, 1968) but none of them published a picture of live specimens.

About half of the range of the genus *Chromaphyosemion* (Togo to Niger delta) is inhabited by only one species, *C. bitaeniatum*, whereas the highest diversity is found in the relatively small area of the coastal plains of Cameroon. In Gabon only two species are found. The diversity reaches its maximum between the River Cross (Nigeria / Cameroon) and the River Ntem (Cameroon / Equatorial Guinea) with 13 species. Especially north of the Sanaga and south of the Kienke the diversity of species is very high, which correlates with the assumed forest refuges in the northern and southern part of Cameroon (Hamilton & Taylor 1991, Maley 1991). The postulated correlation between the assumed rainforest refuges in that area (Lèvêque 1997, Maley 1991) and diversity of species can be confirmed. The diversity north of the Sanaga to the Cross (7 species) can be explained by the rainforest refuge which is postulated by Maley (1991). It was possibly subdivided at the western slopes of the Cameroon backbone and at Mount Cameroon into small rainforest pockets. South of the Kienke six species are found. Maley (1991, fig.6) and Hamilton & Taylor (1991, fig.4) indicate a refuge south of the Sanaga reaching the border of Equatorial Guinea. This area is geographically more structured than

the part between the Sanaga and the Kienke, which could contribute to isolated pockets of rainforest where the species were separated (Amiet 1987, plates 1 and 2). The species expanding in the area between the Sanaga and the Kienke are *C. sp. aff. splendopleure* 'Dizangué', which is at present only known from around Douala to the north of the Kienke, and *C. loennbergii*, which reaches the Sanaga as the northern border of its range. Both populations from the north of the *C. riggenbachii* area (Amiet 1987) need to be studied to verify their inclusion in *C. loennbergii*.

Hamilton & Taylor (1991) postulate a forest refuge in the Niger delta, in which *C. bitaeniatum* could have survived during glacial times and later expanded to the west. The small variation throughout this huge distribution area may indicate a very recent recolonization.

In Gabon, the species might have survived in forest refuges on the slopes of the Monts de Cristal (Hamilton & Taylor 1991, Maley 1991).

If we assume that *C. bivittatum*, *C. sp. 06* and *C. lugens* are closely related species than we can observe two different patterns of isolation / speciation. *C. lugens* and *C. sp. 06* are found in the area of one assumed rainforest refuge which, at least for these species, seems to be subdivided, thus allowing the separation into different species. On the other hand *C. bivittatum* has also split, but in a different refuge. This implies an ancient distribution area between both forest refuges in the north and in the south, which in glacial times was interrupted and afterwards only partly recolonized. It will be of interest to know if species pairs are more common between or within rainforest refuges.

The distribution data show a considerable correlation between areas of species diversity and assumed rainforest refuges, at least in the area of Cameroon. An ongoing study of the phylogeny and biogeography of this genus should give further insight into the structure of the refuges and their influence on speciation.

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References

- Ahl, E. (1924): Neue afrikanische Zahnkarpfen aus dem zoologischen Museum Berlin. – Zool. Anz. 61(3-4):135-145.
- Ahl, E. (1935): Über neue oder seltene afrikanische Zahnkarpfen der Gattungen *Aphyosemion* und *Nothobranchius*. – Zool. Anz. 112:123-129.
- Amiet, J.L. (1987): Fauna of Cameroon. 2 The Genus *Aphyosemion* Myers (Pisces, Teleostei, Cyprinodontiformes). – Sciences Nat, Compiègne.

- Amiet, J.L. (1991): Diagnoses de deux espèces nouvelles d' *Aphyosemion* du Cameroun (Teleostei: Aplocheilidae). – Ichthyol. Explor. Freshwaters 2:83-95.
- Daget, J., J.P. Gosse & D.E.F. Thys van den Audenaerde (eds.) (1986): CLOFFA II Check-List of Freshwater Fish of Africa. – ISNB, MRAC, ORSTOM, Bruxelles.
- Eberl, W. (1996): Die Untergattung *Chromaphyosemion*. – DKG-Journal Supplementheft Nr. 4.
- Eigelshofen, W. & R. Sonnenberg (1999): Kritische Anmerkungen zu " *Aphyosemion kouamense* n. sp., ein neues *Chromaphyosemion* (Teleostei: Aplocheilidae) vom Rand der Monts de Cristal im Nordwesten Gabuns" (DKG-Journal, Heft 2, April 1999). – DKG-Aktuell 3/1999:6-8.
- Hamilton, A.C. & D. Taylor (1991): History of climate and forests in tropical Africa during the last Million years. – Climate Change 19: 65-78.
- Huber, J.H. (1977): Liste nominale annotée de *Aphyosemion* – Myers. Avec description de *Raddaella* et *Kathetys* deux sous-genres à la biologie originale. – Supplement Killi Revue 4.
- Huber, J.H. (1996): Killi-Data 1996. 2nd ed. – Société Française d'Ichthyologie, Paris.
- Huber, J.H. (1998a): *Aphyosemion alpha* n. sp. – Eine neue Art der Untergattung *Chromaphyosemion* mit einem ausgeprägten Färbungsmuster und einer besonders südlichen Verbreitung. – Das Aquarium Nr. 350:15-23.
- Huber, J.H. (1998b): Comparision of Old World and New World Tropical Cyprinodonts. – Société française d'Ichthyologie, Paris.
- Huber, J.H. & L. Seegers (1977): Vorläufige Beschreibung von *Diapteron* nov. subgen. – DKG-Journal 9(9):146-148.
- Kottelat, M. (1976): Modifications taxonomiques au sein des Super-espèces *Aphyosemion gardneri* et *A. walkeri*, avec une Espèce et une Sous-espèce "nouvelle" mais connues et un Sous-genre nouveau. – Aquarama 10(39):23-28.
- Langton, R.W. (1996): Wild Collections of Killifish 1950-1995. – 2nd ed., The American Killifish Association, Mishawaka.
- Legros, O. (1999): *Aphyosemion kouamense* n. sp., ein neues *Chromaphyosemion* (Teleostei: Aplocheilidae) vom Rand der Monts de Cristal im Nordwesten Gabuns. – DKG-Journal 31(2): 32-40.
- Lévêque, C. (1997): Biodiversity dynamics and conservation. The freshwater fish of tropical Africa. – Cambridge University Press, Cambridge.
- Maley, J. (1991): The African rain forest vegetation and paleoenvironments during late Quaternary. – Climatic Change 19:79-98.
- Mayr, E. & R.J. O'Hara (1986): The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. – Evolution 40:55-67.
- Murphy, W.J., & G.E. Collier (1999): Phylogenetic Relationships of African Killifish in the Genera *Aphyosemion* and *Fundulopanchax* Inferred from Mitochondrial DNA Sequences. – Mol. Phyl. Evol. 11:351-360.
- Myers, G.S. (1924): A new Poeciliid fish from the Congo, with remarks on Funduline genera. – Am. Mus. Nov. 116:9pp.

- Radda, A.C. (1971a): Cyprinodontidenstudien im südlichen Kamerun 1. Das Gebiet um Kribi. – *Aquaria* 18: 77-87.
- Radda, A.C. (1971b): Cyprinodontidenstudien im südlichen Kamerun 2. Das Tiefland der Küste. – *Aquaria* 18: 109-121.
- Radda, A.C. (1975): Cyprinodontiden-Studien im südöstlichen Nigeria. I. Die Küstenebene. – *Aquaria* 22: 65-72.
- Radda, A.C. (1977): Vorläufige Beschreibung von vier neuen Subgenera der Gattung *Aphyosemion* Myers. – *Aquaria* 24:209-216.
- Radda, A.C. (1997). *Aphyosemion volcanum* Radda & Wildekamp (1977). – *DKG-Journal* 29(5):106-109.
- Radda, A.C. & J.H. Huber (1976): Cyprinodontiden-Studien in Gabun I. Allgemeines – Nordgabun. – *Aquaria* 23: 179-189.
- Radda A.C. & E. Pürzl (1977): Cyprinodontiden-Studien in Gabun. II. Nordgabun. – *Aquaria* 24: 21-31.
- Radda, A.C. & E. Pürzl (1981): Killifische aus aller Welt. Feldführer der Cyprinodontiformes der Länder der Regenwaldlücke Westafrikas, Band 1 (Togo, Benin, SW-Nigeria). – Otto Hofmann, Wien.
- Radda, A.C. & E. Pürzl (1982): Killifische aus aller Welt. Feldführer der Cyprinodontiformes der Länder der Bucht von Biafra, Band (SO-Nigeria, West-Kamerun). – Otto Hofmann, Wien.
- Radda, A.C. & E. Pürzl (1987): Colour Atlas of Cyprinodonts of the Rain Forest of Tropical Africa. – Otto Hofmann, Wien.
- Radda, A.C. & R.H. Wildekamp (1977): Die *Aphyosemion bivittatum* – Superspecies. – *DKG-Journal* 9: 133-141.
- Roman, B. (1971): Peces de Rio Muni, Guinea Ecuatorial (Aguas dulces y salobres). – *Fondacio La Salle de Ciencias naturales*, Barcelona.
- Sayer, J.A., C.S. Harcourt & N.M. Collins (eds) (1992): The Conservation Atlas of Tropical Forests. Africa. – Macmillan, London.
- Scheel, J.J. (1966): Notes on the phenotype, distribution, and systematics of *Aphyosemion bivittatum* (Lönnberg), with remarks on the Chromosome number in the Rivulinae. – *Ichthyologica (The Aquarium Journal)* 38(3): 261-278.
- Scheel, J.J. (1968): Rivulins of the Old World. – T.F.H. Publ., Neptune City.
- Scheel, J.J. (1972): Fische von Fernando Poo. – *Aquarien und Terrarien* 19:12-13, 46-47, 84.
- Scheel, J.J. (1974): Rivuline Studies. Taxonomic Studies of Rivuline Cyprinodonts from Tropical Atlantic Africa (Rivulinae, Cyprinodontidae, Atheriniformes, Pisces). – *Musee Royal de l’Afrique Centrale, Tervuren, Belgique: Annales, Serie IN-8°, Sciences Zoologiques*, n° 211.
- Scheel, J.J. (1990): Atlas of Killifish of the Old World. – T.F.H. Publ., Neptune City.
- Schröder, B. (1967): Untersuchungen an Gonaden afrikanischer Zahnkarpfenbastarde des *Aphyosemion-bivittatum*-Formenkreises. – *Hausarbeit in Biologie. Univ. Hamburg (unpubl.)*, 47 pp.
- Seegers, L. (1981): *Chromaphyosemion* – kleine Farbwunder aus Westafrika. – *DATZ* 34(5): 155-163.

- Seegers, L. (1986): Bemerkungen über die Sammlung der Cyprinodontiformes (Pisces: Teleostei) des Zoologischen Museums Berlin. I. Die Gattungen *Aphyosemion* Myers, 1924 und *Fundulosoma* Ahl, 1924. Teil 1. – Mitt. Zool. Mus. Berlin 62 (2): 303-321.
- Seegers, L. (1997): Killifish of the World – Old World Killies I. – A.C.S. Glaser, Mörfelden-Walldorf.
- Teugels, G.G., G. McG Reid & R.P. King (1992): Fish of the Cross River Basin (Cameroon-Nigeria) Taxonomy, Zoogeography, Ecology and Conservation. – Musée Royale de l'Afrique Centrale, Tervuren, Belgien, Annales Sciences Zoologiques Vol. 266.
- Thys van den Audenaerde, D.F.E. (1967): The Freshwater Fish of Fernando Poo. – Verhand. Kon. Vlaamse Akad. Klasse Wetenschap 19, No. 100, Brussel.
- Thys van den Audenaerde, D.F.E. (1968): Addendum to the "Freshwater Fish of Fernando Poo". On some fish collected by Col. J.J. Scheel. – Rev. Zool. Bot. Afr. 78(1/2): 123-128.
- Vlaaming, J. (1998): Georg Zenker, wie is dat? – Killi Nieuws 28 (4): 65-76.
- Wildekamp, R.H. (1993): A World of Killies – Atlas of the Oviparous Cyprinodontiform Fish of the World. – The American Killifish Association, Mishawaka.

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THE ALSCO CAMEROON HERPETOLOGICAL EXPEDITION 1998: THE SAMPLING OF A MOUNTAIN RAINFOREST

Hans-Werner Herrmann, Wolfgang Böhme & Patricia Herrmann

Abstract: A herpetological survey of Mt Nlonako, Cameroon, was conducted in November-December 1998. Sampling techniques such as hand capture, glue traps, drift fence / pitfall traps and quadrat sampling were applied. Quantitative and nonquantitative data were gathered. Hand capture and quadrat sampling proved to be the most effective approaches. A total of 40 amphibian and 41 reptilian species were found. In the quadrats amphibians dominated the samples with 80% of all species. Arthroleptidae and Ranidae accounted for 60% of all species. A specimen abundance of 24.1 specimens per 100 m² was found. This exceeds published numbers for rainforests in Borneo, Costa Rica, Panama and previously for Cameroon.

Key words: Cameroon, herpetofauna, quadrat method, drift fence, glue traps, relative specimen abundance, species diversity

Introduction

In November-December 1998 a survey of the herpetofauna of Mt Nlonako, Cameroon (fig.1), was conducted as part of a large scale nature conservation project. Systematic surveys of Cameroon's herpetofauna are urgently needed to obtain information on species distribution and habitat requirements. Such information is vital for successful conservation management and is a keystone for further programs to monitor populations and obtain data on population shifts. Sound data on local population dynamics can be used comparatively and aid in the recognition of potentially endangered systems. Until this study very little was known about the herpetofauna of the Mt Nlonako region. Neighbouring mountain ranges, such as Mt Kupe, were herpetologically surveyed recently (Euskirchen 1998, Schmitz 1998).

Materials and Methods

The survey site is located in southwestern Cameroon, east of Mt Kupe and the Manenguba mountains, in the vicinity of Nkongsamba (fig.1). This forest area also adjoins the remote villages of Nguengue and Eyimba. The site's coordinates are 4°52-55'N and 9°57-59'E (Garmin® GPS 12). The altitude covered ranges from 700 m at Eyimba to a 1600 m mountain peak. The vegetation consists of primary and secondary montane tropical rainforest. Mt Nlonako forests are threatened by clear-cutting for plantations. In-forest disturbance includes hunting and trapping.

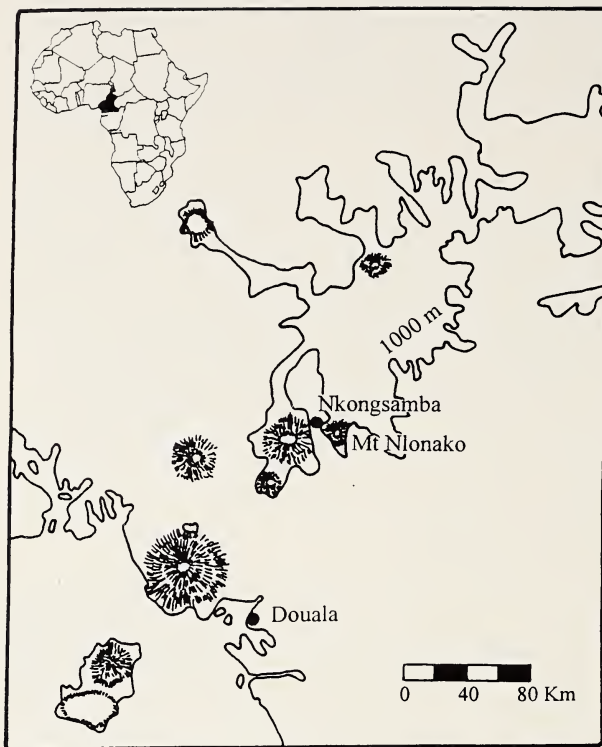


Fig.1: Map of the southwestern Cameroon highlands (revised after Eisentraut 1973).

Many snares and pitfall traps were encountered during our study. However, this area remains species rich; large mammals such as elephants and chimpanzees are still reported. The survey was conducted between the 23th November and 7th December 1998; this is the beginning of the dry season (Müller 1996).

Temperature and relative humidity data were collected by using Hobo® Pro Series Temp + RH dataloggers at three different elevations (700 m, 1200 m, 1600 m). Dataloggers were positioned in the shade on tree trunks at two meters above the ground. Temperatures were recorded every minute for the duration of the study and ranged over 20-27°C at 700 m, 16-25°C at 1200 m and 16-23°C at 1600 m.

Specimens were collected by hand captures, glue traps, drift fence/pitfall traps and quadrat sampling. Hand capture was executed by both scientific staff and local villagers. A total of 42 glue traps (Victor® mouse glue traps) were arranged in an approximately 1 km transect extending from the centre of a plantation into the depths of the forest. The traps were set in pairs at a height of 50 cm and 150 cm on trees of varying diameter. A total of four drift fence-pitfall trap lines were installed in four different habitats (Corn 1994). Drift fences were erected in a Y-shape with each arm of the Y extending 5 m. At the end of each arm and in the centre a 20 l bucket was buried as a pitfall trap. Ten 8 x 8 m (64 m²) quadrat plots were sampled (Jaeger & Inger 1994). Areas were marked and a 1 m perimeter was cleared around the plot before sampling began. Vegetation (with the exception of trees > 10 cm diameter) and leaf litter were removed simultaneously from all four sides, starting at the perimeter and working inward.

Table 1: Description of the ten sampling quadrats with the represented number of amphibian and reptile species each.

Quadrat no.	altitude m a.s.l.	short description	sampling date	no. of amphib. species	no. of reptile species
1	1200	forest between camp and plantation	25-11-98	8	0
2	1200	ecocline: forest to plantation	26-11-98	6	2
3	1600	sunpatch, montane forest	27-11-98	1	0
4	1600	ecocline: fern meadow to montane forest	28-11-98	0	2
5	700	Eyimba, secondary forest	30-11-98	6	0
6	700	Eyimba ecocline: sec. forest to plantation	1-12-98	6	1
7	1200	forest on creek side	2-12-98	10	1
8	1200	forest on creek side	3-12-98	5	0
9	1200	hilltop, tree island in plantation	4-12-98	0	0
10	1200	forest	5-12-98	3	0

Results and Discussion

Hand capture

Although not quantitative, this is a very successful method. Generally hand capture is often the most effective method of accumulating the most species in the minimum amount of time (Scott 1994). This technique resulted in a total of 40 amphibian species in five families and 41 reptile species in 13 families.

Glue traps

Despite precipitation the glue traps maintained their stickiness throughout the duration of the study. However they proved to be largely ineffective, catching a total of only four lizards (*Agama* and *Mabuya*), all found within the sunny plantation area. Insects were often represented as well as feathers of several bird species and one live bat.

Drift fence-pitfall traps

Drift fences with pitfall traps have been used successfully to determine species richness and to detect the presence of rare species (Corn 1994). Here this method proved marginally effective, producing one snake (*Natriciteres*), two lizards (*Panaspis*) and six frogs (*Arthroleptis*, *Phrynobatrachus*). A limitation of this method is that such traps tend to capture some species more readily than others (Corn 1994). Parris et al. (1999) found drift fence-pitfall traps much less effective than stream-searching during their amphibian survey in Queensland, Australia.

Table 2: Number of specimens of amphibians and reptiles found in the 10 sampling quadrats. Uncertain species determination (cf.) is indicated by °, juveniles are indicated by *.

	1	2	3	4	5	6	7	8	9	10
Amphibia	13	23	4	0	24	21	38	11	0	6
Bufonidae	1	1	0	0	8	6	6	0	0	0
<i>Nectophryne afra</i>						5				
<i>Nectophryne batesi</i>		1			8*	1				
<i>Wolterstorffina parvipalmata</i>	1						6			
Arthroleptidae	4	17	4	0	13	10	17	5	0	2
<i>Arthroleptis adelphus</i>	1					3				
<i>Arthroleptis cf. adolfifridgerici</i>			4							
<i>Arthroleptis bivittatus</i>		1*			2					
<i>Arthroleptis poecilinotus</i>		1*			6	5				
<i>Arthroleptis variabilis</i>	2				1					
<i>Arthroleptis</i> sp.		15*			4*	2	12*	2*		
<i>Astylosternus diadematus</i>										1
<i>Astylosternus montanus</i>							2			1
<i>Cardioglossa melanogaster</i>								1		
<i>Leptodactylodon bamilekianus</i>							1			
<i>Leptodactylodon mertensi</i>	1						2	2		
Ranidae	3	0	0	0	0	0	13	6	0	4
<i>Dimorphognathus africanus</i>								2		
<i>Petropedates parkeri</i>							1			
<i>Phrynobatrachus cricogaster</i>							1			
<i>Phrynobatrachus wernerii</i>	1°						7	4		4
<i>Phrynobatrachus</i> sp.	2									
<i>Phrynodon sandersoni</i>							4			
Hyperoliidae	5	5	0	0	3	5	2	0	0	0
<i>Hyperolius ocellatus</i>		1*								
<i>Leptopelis brevirostris</i>	4									
<i>Leptopelis calcaratus</i>	1*	4*			3*	5*	2			
Reptilia	0	2	0	8	0	1	3	0	0	0
Chamaeleonidae	0	1	0	0	0	0	0	0	0	0
<i>Chamaeleo montium</i>		1								
Scincidae	0	0	0	7	0	1	3	0	0	0
<i>Panaspis amietii</i>							3			
<i>Panaspis reichenowii</i>						1				
<i>Panaspis vigintiserierum</i>				7						
Colubridae	0	1	0	1	0	0	0	0	0	0
<i>Chamaelycus fasciatus</i>				1						
<i>Lycophidion laterale</i>		1								

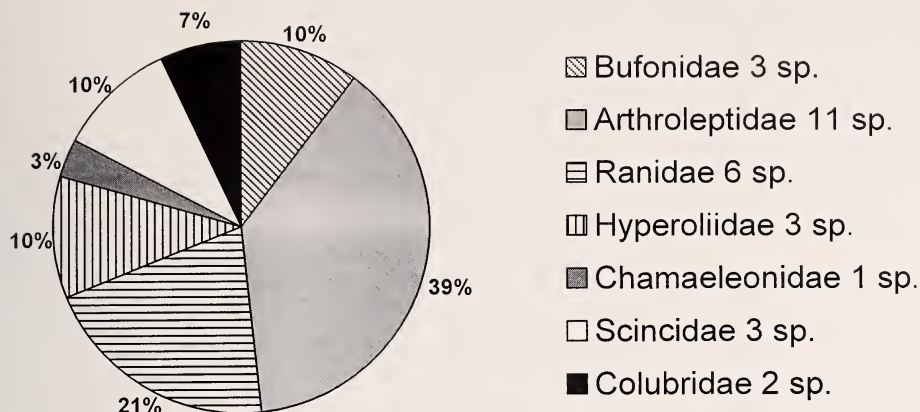


Fig.2: Herpetofauna diversity of all quadrats arranged in families

They found only two species using the traps versus 13 species by stream-searching. Both trapped species were ground-dwellers whereas a high percentage of the species recorded while stream-searching were tree frogs. Additionally, 20 shrews and rodents were also captured in the Mt Nlonako study as well as some terrestrial crabs.

Quadrat sampling

This quantitative method proved to be effective especially for the sampling of leaf litter- and ground-dwelling species (tables 1 and 2). Quadrat sampling yielded 23 amphibian species in four families, whereas hand captures, for comparison, produced 40 species in five families. Fifty-eight percent of the hand captured amphibian species were found in the quadrats. Only 15% of the hand captured reptile species (41 species from 13 families) were represented in the quadrats (six species in three families).

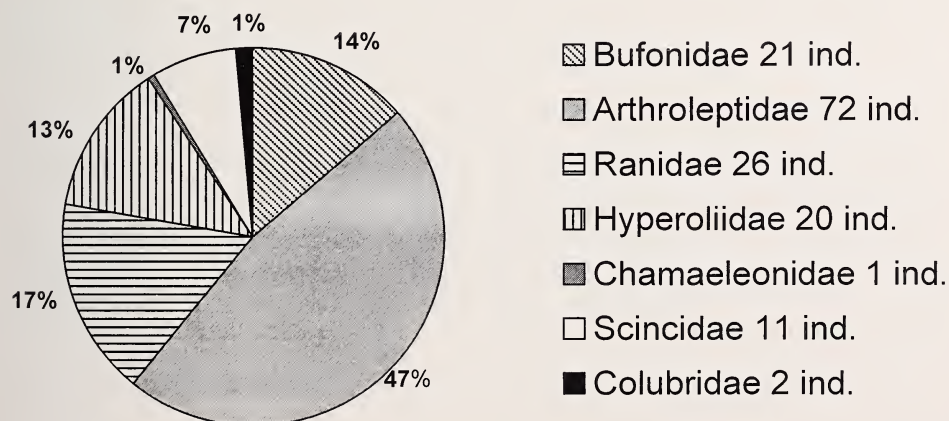


Fig.3: Relative abundance in all quadrats according to family.

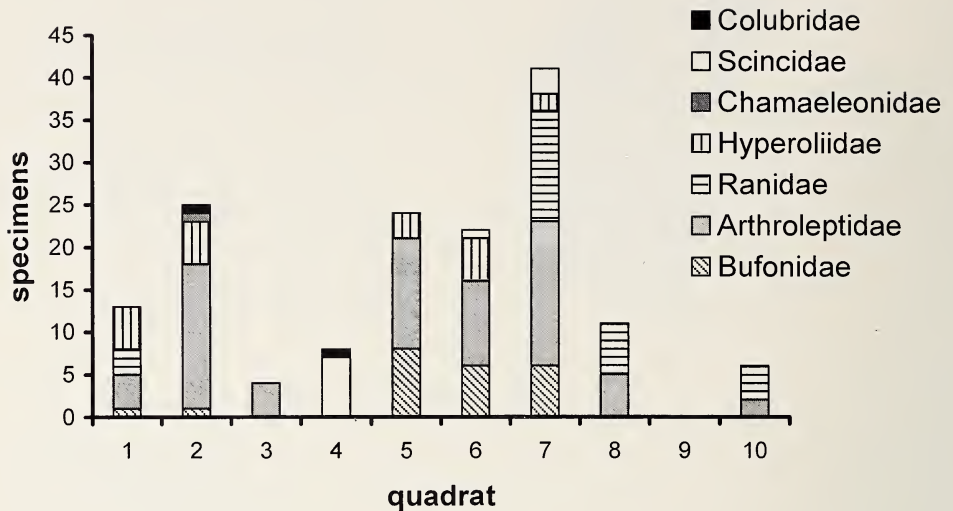


Fig.4: Diversity of amphibian and reptile species per family and quadrat.

Reptiles represented 20% of all herpetological species (fig.2) found in the quadrats and nine percent of all herpetological specimens (fig.3). Quadrat four (1600 m elevation) contained reptiles but no amphibians (table 2, fig.4 and 5). This can be related to the fact that there was no running or open water at this altitude, thus restricting amphibians dependent upon such water for reproduction. Quadrat 3 (1600 m elevation), however, contained four specimens of *Arthroleptis* cf. *adolffriderci*. This species does not require water bodies for reproduction because it lays its eggs in moist substrate (Duellman & Trueb 1986). A similar case is reported from America, where *Eleutherodactylus*, which also undergoes a development independent of free water, may even ecologically replace small lizards (Scott 1976a). Accordingly, Inger (1980) reports that in South-east Asia and Central America floor-dwelling species of frogs and lizards in tropical forests are ecologically very similar. Quadrats 3 and 4 are characterized by low species diversity and low specimen abundance (fig.4 and 5).

Arthroleptidae and Ranidae accounted for 60% of all species (fig.2) and 64% of all reported specimens (fig.3). Arthroleptid specimens represented almost half (47%) of all specimens found and were present in eight out of ten plots.

Interestingly, hyperoliids were found only in quadrats where bufonids were present as well (figs.4 and 5). The reason may be that all reported toads were at least partially arboreal species and thus somewhat similar to treefrogs in their habitat requirements.

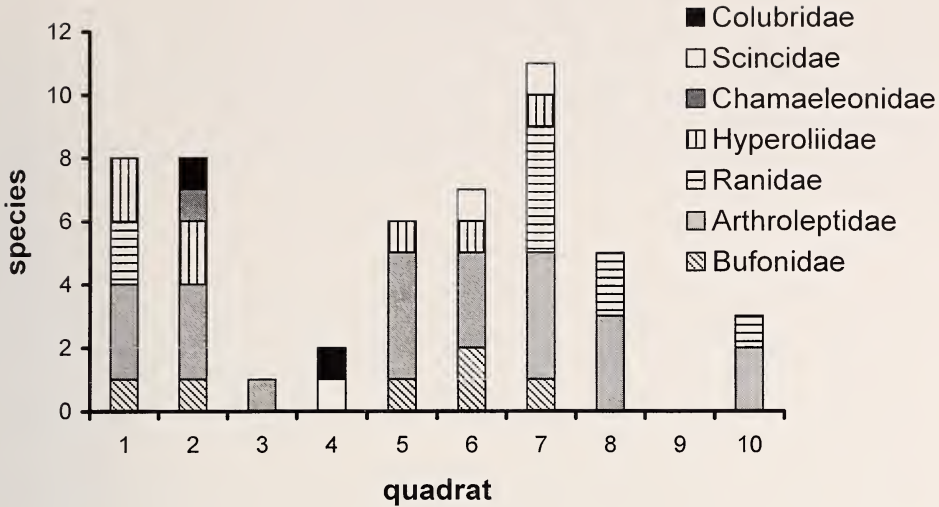


Fig.5: Abundance of individuals per family and quadrat.

Quadrat 7 had the highest species diversity and specimen abundance (figs.4 and 5). This can be explained by its position at a creek and its possibly higher microhabitat diversity. However, such an explanation may be wrong since quadrat 8, an apparently similar plot, produced only average diversity and less than average abundance values.

In general, quadrats varied greatly with regard to species diversity and specimen abundance. Thus conclusions drawn from statistical analysis of results obtained by the quadrat method will show significant trends only when larger numbers of quadrats are investigated (at least 50 quadrats; Jaeger & Inger 1994).

The lack of animals in quadrat 9 can only be explained by variation within the samples.

Scott (1976b) found a total of eight species of three amphibian families (Bufonidae, Arthroleptidae, Ranidae) in 15 rainforest plots in the Cameroon lowland (up to 30 m elevation). Quadrat size was 58 m². Specimens of Arthroleptidae greatly outnumbered Bufonidae and Ranidae.

In the Mt Nlonako study a total of 24.1 specimens/100 m² were found; amphibians with 21.9 and reptiles with 2.2 specimens/100 m². Scott (1976b) noted 9.4 individuals/100 m² in his Cameroon lowland rainforest study area. He reports 1.5 specimens/100 m² for a Bornean site, and in Central America 14.6 (Panama) and 17.1 (Costa Rica) individuals/100 m². This clearly means that the Mt Nlonako abundances are even higher than the Central American herpetofauna abundances studied so far.

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References

- Corn, P.S. (1994): Straight-Line Drift Fences and Pitfall Traps. – pp. 109-117 in: *Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians* (eds. Heyer, W.R., et al.). – Smithsonian Institution Press.
- Duellman, W.E. & L. Trueb (1986): *Biology of Amphibians*. – McGraw-Hill Book Company, New York.
- Eisentraut, M. (1973): Die Wirbeltierfauna von Fernando Poo und Westkamerun. – Bonn. zool. Monogr. 3: 1-428.
- Euskirchen, O. (1998): Untersuchungen zur Ökologie und Ethologie der Herpetofauna einer montanen Regenwaldregion in Kamerun. – Unpublished Master's Thesis, Universität Bonn, 176 pp.
- Inger, R.F. (1980): Densities of floor-dwelling frogs and lizards in lowland forests of Southeast Asia and Central America. – *The American Naturalist* 115: 761-770.
- Jaeger, R.G. & R.F. Inger (1994): Quadrat sampling. – pp. 97-106 in: *Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians* (eds. Heyer, W.R., et al.). – Smithsonian Institution Press.
- Müller, M.J. (1996): *Handbuch ausgewählter Klimastationen der Erde*. – Forschungsstelle Bodenerosion, Universität Trier, Heft 5: 400 pp.
- Parris, K.M., Norton, T.W. & R.B. Cunningham (1999): A comparison of techniques for sampling amphibians in the forests of south-east Queensland, Australia. – *Herpetologica* 55: 271-283.
- Schmitz, A. (1998): Systematik und Zoogeographie der Herpetofauna einer montanen Regenwaldregion in Kamerun. – Unpublished Master's Thesis, Universität Bonn, 261 pp.
- Scott, N.J. (1976a): The abundance and diversity of the herpetofauna of tropical forest litter. – *Biotropica* 8: 41-58.
- Scott, N.J., Jr. (1976b): The herpetofauna of forest litter plots from Cameroon, Africa. – pp. 145-150 in: *Herpetological communities* (ed. Scott, N.J., Jr.). – U.S. Department of the Interior, Fish and Wildlife Service, Wildlife Research Report 13.
- Scott, N.J., Jr. (1994): Complete species inventories. – pp. 78-84 in: *Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians* (eds. Heyer, W.R., et al.). – Smithsonian Institution Press.

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New record of Grauer's Blind Snake *Rhinotyphlops graueri* (Sternfeld, 1912) (Reptilia: Serpentes: Typhlopidae) in western Uganda

Jan R. Šlapeta, Petr Nečas & David Modrý

Abstract: During a herpetological excursion to Western Uganda in August 1996, one specimen of *Rhinotyphlops graueri* (Sternfeld, 1912) was collected. The specimen was found dead in a shallow periodic water pool in the remaining rain forest on the pathway in the Semuliki National Park (0°50'N 30°5'E). The reported specimen is 271 mm long and 4.2 mm wide (at midbody) and has 24 scale rows at midbody. The head, with a rounded slightly prominent snout, is indistinct from the neck. The specimen is deposited in Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK 63.138). The presented finding is situated about 500 km north of the previous northernmost record and represents the first report of *Rhinotyphlops graueri* (Sternfeld, 1912) from Uganda. There is no evidence of a geomorphological or ecological border between the previously published localities and this new record, which lies just on the eastern margin of the Congo basin.

Key words: *Rhinotyphlops graueri*, new record, Uganda

Introduction

Rhinotyphlops graueri was originally described as *Typhlops graueri* by Sternfeld (1912). The type locality is originally mentioned as "Ufer des Tanganyika, Urwald hinter den Randbergen am Nordwestufer des Tanganyika". Laurent (1956) synonymized *Typhlops avakubae* Schmidt, 1923 with *T. graueri* Sternfeld, 1912, but this was stated as an error by Roux-Estève (1974) who synonymized *T. avakubae* Schmidt, 1923 with *Rhinotyphlops caecus* (Duméril, 1856). Finally, Roux-Estève (1974) placed *Typhlops graueri* into the genus *Rhinotyphlops* and considered *T. gracilis polli* Laurent, 1960 (originally described as *T. leptosoma polli* Laurent, 1956) to be its junior synonym. *R. graueri* (Sternfeld, 1912) belongs to the "Group VI" of the african typhlopids (sensu Roux-Estève 1974), together with a further eight species: *R. caecus*, *R. pallidus*, *R. lumbriciformis*, *R. gracilis*, *R. rufescens*, *R. sudanensis*, *R. kibarae* and *R. wittei*, all from tropical equatorial Africa from Fernando Poo (Bioko) to Zanzibar. The recently described *Rhinotyphlops debilis* from the Central African Republic also matches the mentioned "Group VI" (Joger 1990).

During a herpetological excursion to Western Uganda, undertaken by the authors in August 1996, one specimen of *Rhinotyphlops graueri* was found dead in a shallow periodic water pool in tropical rain forest after a heavy night rain on a pathway crossing the Semuliki National Park. The specimen is now deposited at the Zoologisches Forschungsinstitut und Museum Alexander Koenig

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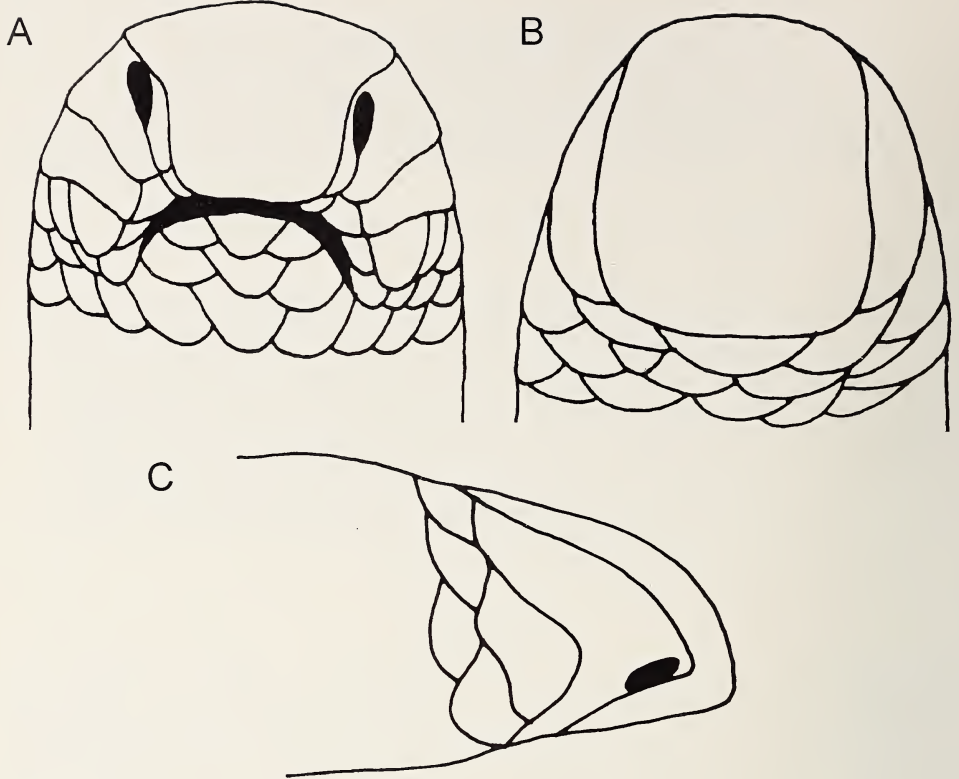


Fig. 1: Line drawing of a head of *Rhinotyphlops graueri* (Sternfeld, 1912), ZFMK 63.138): A: ventral view, B: dorsal view, C: lateral view.

in Bonn (ZFMK¹ 63.138). The collected specimen is 271 mm long and 4.2 mm wide and has 24 scale rows at midbody. The head is indistinct from the neck, with a round, slightly prominent snout (fig.1). The entire body is of a uniform pinkish colour. It is in all characters (sensu Sternfeld 1912, Roux-Estève 1974, Broadley & Howell 1991, Meirte 1992) in accordance with *Rhinotyphlops graueri*, though was discovered out of the known distribution area of this species.

According to Roux-Estève (1974), *Rhinotyphlops graueri* is distributed in central tropical Africa below the equator around Lake Tanganyika in the Democratic Republic of Congo (former Zaïre), Burundi and Tanzania. The northernmost record (RGMC 21495 –496), was collected near Rumonge in Burundi, identified by Roux-Estève (1974) out of 14 examined *Rhinotyphlops* specimens. Further known records come from Burundi (two specimens from one locality), Tanzania (six specimens from two close localities) and the Democratic Republic of Congo (six specimens from four localities) – for details see appendix. The localities in Burundi and Tanzania are located within the remaining rainforest close to the Lake Tanganyika shore. The

¹⁾ The following abbreviations for institutions are used in the text:

ZFMK = Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany

RGMC = Musée Royal de l'Afrique Centrale, Belgium

IRSN = Institut Royal des Sciences Naturelles de Belgique

MCZ = Museum of Comparative Zoology, Harvard University, USA

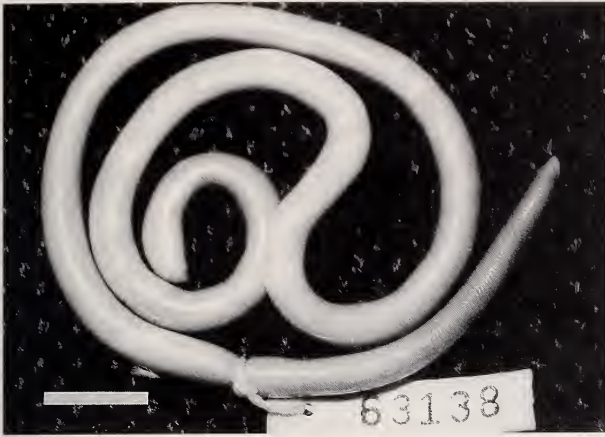


Fig.2: The preserved specimen of *Rhinotyphlops graueri* from Uganda (ZFMK 63.138) - scale bar = 1 cm

localities in the Democratic Republic of Congo lay in the rainforest of the Congo Basin, 300 km west of the Lake Tanganyika shore.

Our specimen was found about 500 km north of the previous northernmost record of *Rhinotyphlops graueri*. The Semuliki National Park is a relatively small area along the river Semuliki within the Ituri forest, belonging to the Congo basin. The fauna and flora of this area consists predominantly of species typical for the Congo basin, with some East African elements. There is no obvious geographical or ecological border between the previously known localities and our new record.

Loveridge (1937) and Laurent (1954) published lists of forest snakes from the area around the "Great Lakes". Both works were commented on by Hughes (1983) in his attempt to summarize the African snake fauna. According to all above-mentioned papers *Rhinotyphlops graueri* belongs to the species which are restricted to forests.

Blind snakes are generally secretive snakes adapted to a fossorial life, usually found on the surface after rains and/or floods. This is the main reason why there are rather limited numbers of specimens in museum collections.

This report extends the distribution range of Grauer's Blind Snake, *Rhinotyphlops graueri*, ca. 500 km northward and represents the first record of this species north of the equator. Additionally, this finding adds a further species to the checklist of Ugandan herpetofauna. It can be expected that the distribution of this species extends along the "Great Lakes" (Tanganyika, Kivu and Edward) in tropical equatorial Africa, being confined to lowland rainforests.

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References

- Broadley, D.G. & K M. Howell (1991): A Check List of the Reptiles of Tanzania, with Synoptic Keys. – Syntarsus 1: 1–70.
- Hughes, B. (1983): African snake fauna. – Bonn. zool. Beitr. 34: 311–356.
- Joger, U. (1990): The herpetofauna of the Central African Republic, with description of a new species of *Rhinotyphlops* (Serpentes: Typhlopidae). – pp. 85–102 in: Vertebrates in the tropics (eds. Peters G. & R. Hutterer). – Alexander Koenig Zoological Research Institute and Zoological Museum, Bonn.
- Laurent, R.F. (1954): Aperçu de la biogéographie des batraciens et des reptiles de la région des grands lacs. – Bull. Soc. zool. France 79 (4): 290–310.
- Laurent, R.F. (1956): Contribution à l'herpétologie de la région des Grands Lacs de l'Afrique centrale. I. Généralités. II. Chéloniens. III. Ophidiens. – Ann. Mus. r. Congo Belg., sér. in-8°, Sci. Zool., 48: 1–390.
- Loveridge, A. (1937): Scientific results of an expedition to rain forest regions in eastern Africa. IX. Zoogeography and itinerary. – Bull. Mus. comp. Zool. Harv. 79: 479–541.
- Meirte, D. (1992): Cles de détermination des serpents d'Afrique. – Ann. Mus. Roy. Afr. Cent. Sér. 8vo, Sci. Zool. 267: 1–161.
- Roux-Estève, R. (1974): Révision systématique des Typhlopidae d'Afrique (Reptilia-Serpentes). – Mém. Mus. Nat. d'Histoire Natur. (N.S.), LXXXVII: 1–313.
- Sternfeld, R. (1912): Reptilia. pp. 197–279 in: Wissenschaftliche Ergebnisse der Deutschen Zentral-Africa Expedition 1907–1908.IV. – Leipzig.

Appendix: Records of *Rhinotyphlops graueri* (Sternfeld, 1912)

Democratic Republic of Congo: RGMC 1.985: (holotype of *T. leptosoma poli*): Katanga, Tanganyika district, ter. Albertville, Niemba; – IRSN 2.057: riv. Lubunduy, ter. Albertville; – RGMC 18.002–18005: (paratypes of *T. leptosoma poli*): Nyunzu, ter. Albertville; – RGMC 15.353: (paratype of *T. leptosoma poli* and *T. kibarae*): Kabalo, ter. Kabalo.

Burundi: RGMC 21.495–496: Rumonge, ter. Bururi.

Tanzania: MCZ 48.051–53: Ujiji; – MCZ 48.054–56: Bagilo–Ujiji.

Uganda: ZFMK 63.138: Semuliki National Park.

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Developmental plasticity and behavioural adaptations of two West African anurans living in an unpredictable environment (Amphibia, Anura)

Marko Spieler

Abstract: In the Comoé National Park in Ivory Coast (West Africa) alternative reproductive strategies of two anuran species were investigated. Laboratory experiments showed that larvae of *Bufo maculatus* responded adaptively to lowered water levels by accelerating their development and metamorphosing smaller and faster than tadpoles grown in constantly high water volumes, whereas larvae experiencing increased water levels did not significantly change growth or developmental rates. First results in *Hoplobatrachus occipitalis* indicate that larvae of this species showed a fixed minimum developmental rate. Only the size at metamorphosis varies according to different water level conditions.

In accordance with the high predation risk by different aquatic predators, two different types of adaptations were found. Tadpoles of *B. maculatus* aggregated in shallow water regions if attacked by cichlid fishes, the most important predators in the river spawning site of this toad species. These shallow areas are not accessible to the larger-sized predators. Experiments to determine the mechanism of aggregation behaviour showed that an alarm pheromone from injured *B. maculatus* tadpoles in combination with a mechanosensitive cue from rapid movements of aquatic predators elicits aggregation behaviour in conspecific tadpoles. The most important predators in the little rock pools, the main spawning site of *H. occipitalis*, are carnivorous conspecifics. The adults minimize the risk of cannibalism of their tadpoles by preferring of pools as spawning sites that have no or only few other conspecific tadpoles. Experiments showed that the density as well as the size of conspecific larvae in a pond is determined by the adults via chemical cues.

Key words: *Hoplobatrachus occipitalis*, *Bufo maculatus*, phenotypic plasticity, reproductive strategy, aggregation behaviour, environmental stress

Introduction

Thirty-four anuran species are known from the Comoé National Park in Ivory Coast (West Africa) (Rödel 1996). In view of such a high number of species in a small area, different reproductive strategies to reduce competition can be expected (Mayhew 1968). The choice of different spawning sites is one of the potential possibilities (Resetarits and Wilbur 1989, Resetarits 1996). Therefore different adaptations to the specific conditions of the breeding sites utilized are to be expected. While most of the 34 anuran species breed in ephemeral savannah ponds, three frog species bred in two alternative spawning sites that were completely different to that of the savannah (Spieler 1997a).

Bufo maculatus and *B. regularis* use shallow depressions on the flooded river plains with quickly changing water levels as their main breeding habitat. There the tadpoles have to cope with two main problems:

1) high desiccation risk once the larval habitat becomes isolated from the river,

2) heavy and unpredictable predation risk by cichlid fish that invade the breeding habitats when the river water level increases, leaving again when the water level decreases.

Occasionally, these spawning sites allowed very successful breeding, but usually complete reproductive failure occurred (Linsenmair 1998).

Hoplobatrachus occipitalis breeds at the very beginning of the rainy season in little pools on rocky river banks that are already completely filled after small amounts of the first local rainfall. If there is no additional precipitation during the next few days these little rock pools dry out completely. In contrast, the bigger savannah ponds did not exist at this early time. Only after several heavy rains the savannah soil is saturated with water, the ponds are filled and remain for longer periods. Then they are used as spawning sites by *H. occipitalis*, as well as by other anuran species in the area. Besides the high risk of desiccation in the rock pools, tadpoles have to cope with the high and long lasting predation risk from conspecifics which drastically increases in times of food shortage. In favourable years breeding in rock pools showed an unusually high reproductive success of more than 30 % survival rate, whereas in unfavourable years over 90% of the breeding pools did not produce a single metamorphosed froglet. In contrast, in the savannah pools the differences in survival rate between years are less pronounced, but usually not more than 2% of the larvae survived (Linsenmair 1998).

The following two questions were at the center of our attention in this study. Do the larvae of *B. maculatus* and *H. occipitalis* respond adaptively to the decreased water levels that indicate the start of desiccation of their larval environment? In other words, do larvae in this situation accelerate their developmental rate at the cost of growth by metamorphosing earlier but at a smaller size than siblings that grow under conditions of constant or increasing water level? Do these larvae respond differently to the different predators, cichlid fish in the case of *B. maculatus* and carnivorous conspecific tadpoles in the case of *H. occipitalis*?

Materials and Methods

Study area

The study was conducted in the Guinean savannah of Comoé National Park (8°5'-9°6'N, 3°1'-4°4'W) in the northeastern part of the Ivory Coast, the largest National Park (11,500 km²) in West Africa. The study area is situated in the immediate surroundings of a research camp of the University of Würzburg. The tree-scrub-savannah in this region is characterized by distinct rainy and dry seasons, with a mean annual precipitation between 750 and 1100 mm during the last 7 years (our own measurements) and on average 1100 mm between 1977 and 1987 (Poilecot 1991). The core dry period lasting from December to February is usually without any precipitation. Most bodies of water in the study area are ephemeral ponds that always dry up in the dry season and usually also several times in the rainy period. River beds of the large rivers are the only places where pools of water persist throughout the dry season. The date of the first rain, as well as the amount and spatial distribution of the following rains at the beginning of rainy season, are extremely variable and unpredictable from year to year.

Studied animals

Bufo maculatus Hallowell, 1854, a medium-sized toad (female: 41–60 mm, $n=5$; male: 40–54 mm, $n=4$) is widely distributed over Africa south of the Sahara. The clutches of *B. maculatus* had 4000–8000 eggs per string ($n=5$). The tadpoles did not disperse far from their hatching site but remained together at the same locality for several days. Larvae feed on algae and detritus. We chose to observe aggregation behaviour in *B. maculatus* instead of *B. regularis* Reuss, 1833 living sympatrically with *B. maculatus* on the banks of the Comoé river because this species was more common in the study area than *B. regularis*.

*Hoplobatrachus occipitalis*¹ (Günther, 1858) is broadly distributed over West Africa (Lamotte 1967). Sexually mature individuals vary greatly in body size (females: 81.8 ± 11.7 mm, range: 59–111 mm, $n=42$; males: 76.8 ± 7.9 mm, range: 65–99 mm, $n=43$). Females attach their eggs, one at a time, to the bottom of shallow areas of pools. The number of mature eggs in the gonads of five medium sized females was 1590 ± 310 . The tadpoles are carnivorous and cannibalistic, preying on insect larvae and tadpoles of conspecifics and other anurans (Spieler & Linsenmair 1997). They have well developed horny jaws with a characteristic spine.

Experimental design to investigate developmental plasticity

In laboratory experiments both individuals and groups of tadpoles were raised under constantly low (LL-treatment group), constantly high (HH), decreased (HL) and increased (LH) water level conditions. The size of aquaria used was 19x9x6 cm. It was not known which water levels represented low or high water conditions for tadpoles. Therefore in one set of experiments, 320 ml of water were used for low water conditions (2 cm water) and 640 ml were used in aquaria with high water conditions (4 cm water). In another set of experiments, 160 ml of water (1 cm water) represented low water conditions and 320 ml (2 cm water) high water conditions. In experiments with individual tadpoles, five aquaria per treatment group were used in the case of *H. occipitalis* and 10 in the case of *B. maculatus*. Experiments with groups of 5 or 10 tadpoles in each aquarium, coming from the same clutch, were made only with *B. maculatus* (10 aquaria/treatment group). The water level was changed in treatment groups HL and LH when tadpoles had reached developmental stage 38 after Gosner (1960) in *B. maculatus* and 34 in *H. occipitalis*. Metamorphosis was reached with developmental stage 46. The water temperature in all experiments was $28 \pm 2^\circ\text{C}$ (daily range: 26–30°C). Every fourth day a complete water exchange was made. The larvae were fed ad lib, *B. maculatus* with Tetra Phyll (dry plants) and cleaned lettuce pieces of 5x5 cm, *H. occipitalis* with mosquito larvae.

Means are given \pm standard deviations. For statistical analysis a STATISTICA/Mac program by StatSoft 1991 was used. The significance level was set at $p < 0.05$ unless stated otherwise.

¹ We have decided to classify this species as part of the genus *Hoplobatrachus* (formerly: *Dicroglossus*) listed by Duellman (1993) in accordance with a revision by Dubois (1992). This decision does not presuppose any intention to support this revision given the present state of knowledge.

Results

Developmental plasticity

Larvae of *B. maculatus* responded adaptively to lowered water levels by accelerating their development and metamorphosing smaller and faster than tadpoles grown in constantly high water volumes. Siblings experiencing increased water levels did not significantly change growth or developmental rates in comparison with tadpoles grown in constantly low water volumes (fig.1).

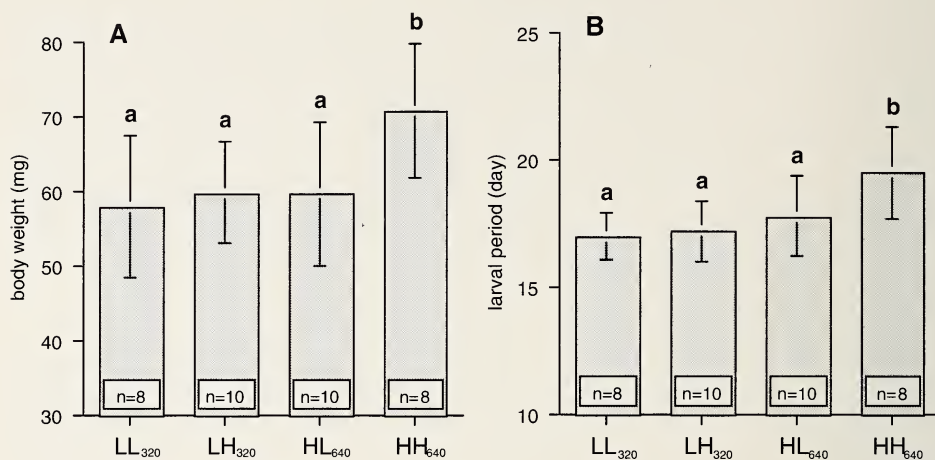


Fig. 1: (A) Mean body mass of different treatment groups of *B. maculatus* at metamorphosis. (B) Mean developmental time from hatching to metamorphosis of the same tadpoles. Different letters above bars indicate significant differences (Tukey-type multiple comparisons).

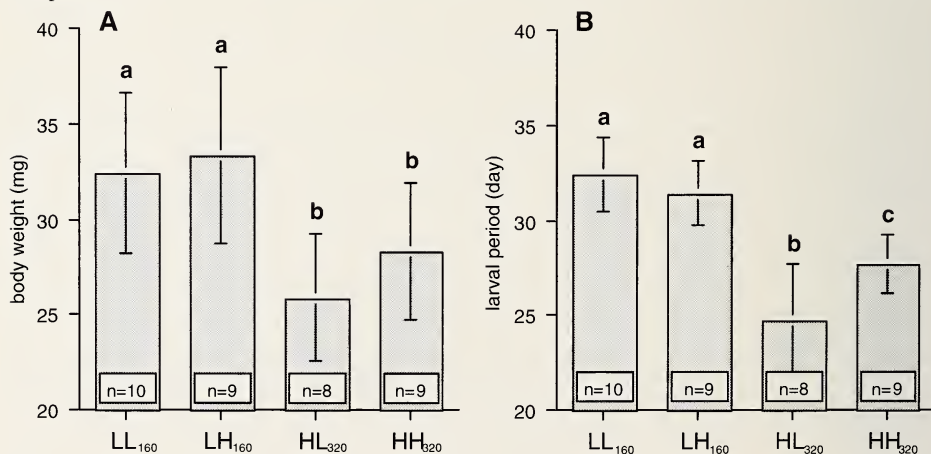


Fig. 2 (A) Mean body mass of the first metamorphosing froglet in each aquarium in the different treatment groups of *B. maculatus*. (B) Mean developmental time from hatching to metamorphosis of the same tadpoles. Different letters above bars indicate significant differences (Tukey-type multiple comparisons).

Similar results were found in experiments in which the water level was changed earlier, at Gosner-developmental stage 34, as well as in experiments in which 160 ml and 320 ml water levels were used (Spieler 1997b). Experiments with groups of *B. maculatus* tadpoles showed that in most cases the first metamorphosing froglet in each aquarium in the HL treatment group was smaller but earlier than the first metamorphosing froglet in each aquarium of the other three treatment groups (fig.2).

Larvae of *H. occipitalis* experiencing decreased water levels metamorphosed at a smaller size; those experiencing increased water levels metamorphosed at a larger size than siblings grown in corresponding constant water levels. Unexpectedly, larvae of all treatment groups showed a similar developmental rate (fig.3).

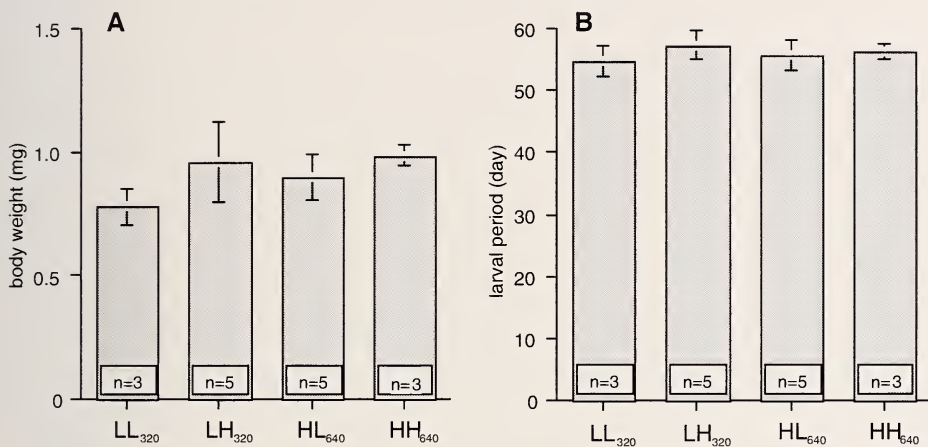


Fig. 3 (A) Mean body mass at, and (B) mean timing of metamorphosis of the different treatment groups of *H. occipitalis* tadpoles. Because of low sample size in some treatment groups no statistical comparisons can be made.

Reaction of tadpoles to different predators

The main spawning sites of *B. maculatus* are shallow depressions on the margins of rivers, where tadpoles of this toad species are either evenly distributed or aggregated. Two types of aggregations were observed. One moving in swarms on the bottom and one stationary, with the latter concentrated on small sections at the edges of puddles in extremely shallow regions of 0.1-0.5 cm of water (fig.4).

The stationary aggregations contained up to several thousand individuals on an area of 10-20 cm in diameter. Observations and exchange-experiments showed that tadpoles formed stationary aggregations in shallow water regions only in the presence of predators (Spieler and Linsenmair 1999). These areas are not accessible to the larger predators. The most frequent predators found were young cichlid fish and at lower abundance the carnivorous tadpoles of *H. occipitalis*.

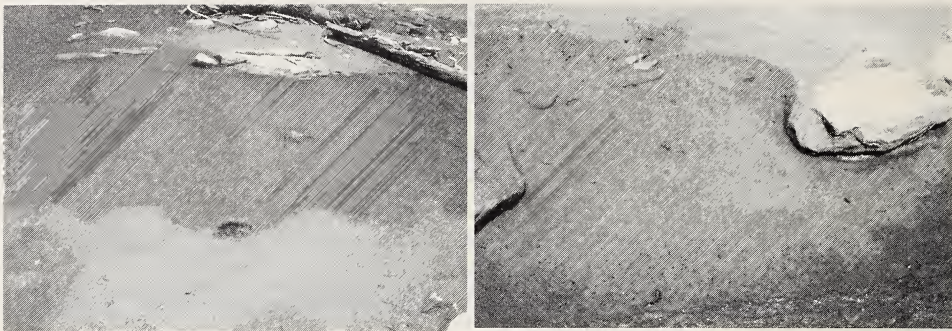


Fig.4: Aggregated (left) and non-aggregated (right) tadpoles of *B. maculatus* in the Comoé river

Semi-natural experiments showed that a species-specific or genus-specific alarm pheromone released by injured *B. maculatus* tadpoles in combination with a mechanosensitive cue from the quick movements of aquatic predators elicits aggregation behaviour in conspecific tadpoles (Spieler & Linsenmair 1999).

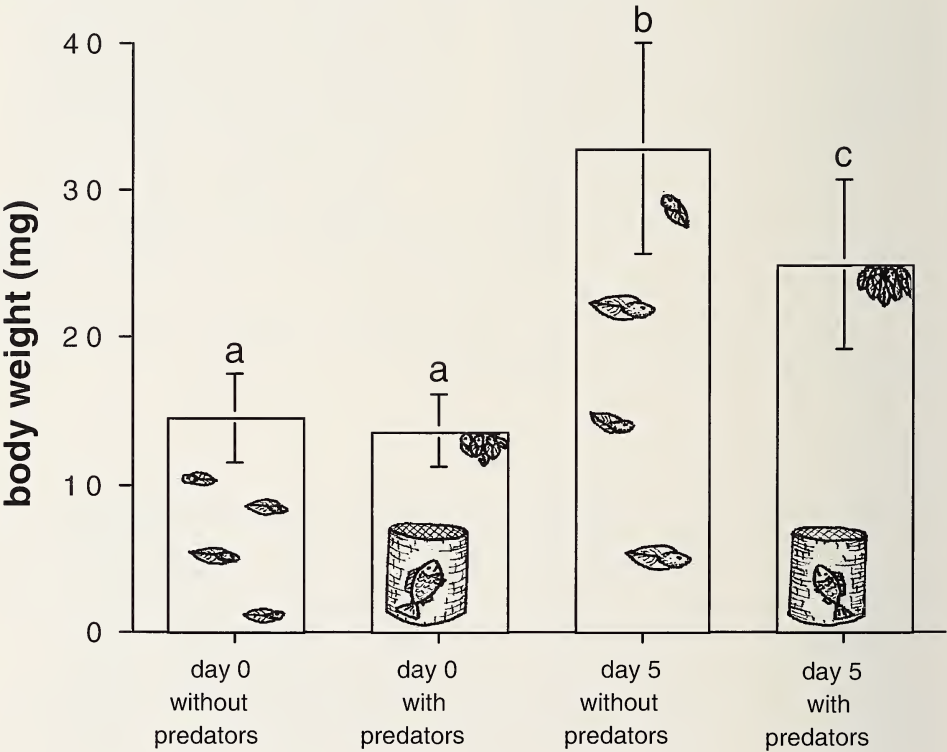


Fig.5: Relationship between mean body mass (+/-SD) of aggregated medium-sized *B. maculatus* tadpoles (aggregation caused by predators) and non-aggregated sibling tadpoles in artificial ponds without predators. After 6 days the mean size of aggregated tadpoles was significantly lower in comparison with non-aggregated larvae (Mann-Whitney U-Test).

Since feeding opportunities should be reduced within a stationary aggregation, spending any extended time aggregated will lead to either a longer developmental time and/or will negatively affect the size at metamorphosis. Groups of tadpoles in natural pools, one aggregated and the other evenly distributed, with an initially identical body mass, showed significant differences in mass gain already after 2 days (Spieler & Linsenmair 1999). Similar results were found in experiments with tadpoles in artificial ponds (fig.5). Cichlids usually leave the puddles when falling water levels reach a critical limit. The aggregated tadpoles then dissolve their aggregations after some hours and begin feeding to an increased extent.

The most effective predators of *H. occipitalis* tadpoles in the rock pools are the carnivorous conspecific larvae (Spieler 1996). Hatchlings have only low survival rate in pools with older conspecifics. Therefore reproducing *H. occipitalis* lay their eggs preferably in breeding ponds containing no or only a few other conspecific tadpoles. Experiments showed that the density of conspecific larvae in a pond is determined by the adults by means of chemical cues (Spieler & Linsenmair 1997).

In addition, adult frogs showed risk-spreading behaviour. Most radio-tracked frogs visited and also spawned in more than one rock pool during one laying bout (Spieler and Linsenmair 1998b). They seemed to spawn only a small fraction of their mature eggs in one night. Only some females, laying during the first spawning bout of the year in the largest rock pool that contained no other conspecific larvae, spawned all their approximately 1600 mature eggs in this pool. When rock pools were flooded by the increasing water level of the river, most *H. occipitalis* left the river bed and migrated to savannah pools. Several individuals travelled distances of up to 6 km and each frog visited thereby up to 10 savannah ponds to spawn there (Spieler 1997c).

Discussion

Sympatrically-living anurans in the study area possess very different life-history strategies (Spieler 1997a, Linsenmair 1998). All these anurans are confronted with one major problem, the unpredictable variability of the rainfall pattern in time and space. For species that produce only few but large eggs, one of the best tactics to confront such unpredictable conditions is to spread the risk by sparingly spending eggs and always retaining enough for the next breeding opportunity, as well as to select only suitable pools as spawning sites by including in their choice all available abiotic and biotic parameters (e.g. size and seepage of pools, density of predators in the pool) that characterize an individual pool (Spieler & Linsenmair 1998a). This strategy seems to have evolved in *H. occipitalis*. Another tactic is to spawn numerous and small eggs and to leave it up to the tadpoles to react to the variable conditions of their environment. This seems to be realized in *B. maculatus*. At the larval stage, the best tactic seems to have a plastic aquatic developmental rate corresponding to water level variations. This strategy seems to have evolved in tadpoles of *B. maculatus*.

Hoplobatrachus occipitalis is the only species in the frog community of the Comoé National Park that breeds regularly after the earliest rains (Spieler & Linsenmair 1997). This is possible because the species uses small rock pools at the river bank as spawning sites that have been completely filled after the first small

rainfalls. But these pools have severe disadvantages for reproducing frogs. Because of the relatively small size of these rock pools compared with the bigger savannah ponds the risk of desiccation is very high. On rocky areas at the river bank of approximately 0.01 km² more than 100 rock pools could be present. The quality of these pools varies to their water depth and seepage. According to the prediction, adult *H. occipitalis* minimize the risk for their tadpoles to dry out by distributing their eggs over several pools and prefer those pools that contain water for a longer period (water-holding capacity: WHC, Spieler & Linsenmair 1997). In addition, adult frogs minimize the risk of their tadpoles to becoming victims of cannibalism by preferring pools as spawning sites that are still unoccupied by conspecific tadpoles (Spieler & Linsenmair 1997). The important role of cannibalism in the survival rate of tadpoles was emphasized by Petranksa & Daphne (1995). But few indications are present that predators influence the choice of spawning sites in frogs (Beebe 1985, Resetarits & Wilbur 1989, Ildas & Ancona 1994).

In contrast, *Bufo maculatus* uses spawning sites on the margins of rivers. The quality of these sites depends on the level of groundwater, the water level of rivers and the amount of local rainfall. If the water level increases, predatory fish can invade the spawning sites, which they have to leave when the water level falls. In view of the quickly and unpredictably changing water level, the quality of these spawning sites is not detectable for frogs at the time of spawning. That is possibly the reason why we found no strong spawning-site selection in this species. Here, the tadpoles have to cope with the high risk of predation and desiccation and have evolved different strategies against these risks. As a reaction to the high predation pressure, tadpoles form in the presence of predators tight and long-lasting aggregations, at the cost of a marked decrease in growth (Spieler & Linsenmair 1999). Similar behaviours are described in a few other anuran species (Bragg 1965, Hews 1988, Caldwell 1989, Waldman 1991, Rödel & Linsenmair 1997).

Developmental plasticity

An further controverse point is, whether developmental rate and growth of tadpoles are strongly coupled and could vary only together in relation with biotic and abiotic parameters or whether developmental rate and growth of tadpoles are more independent and could allow a trade off between this two. It should be highly adaptive in an unpredictable environment to accelerate the developmental rate at the cost of growth and to metamorphose faster but with smaller size in the case of decreasing water level in comparison with siblings that grown under constant or increasing water level conditions after new rain falls (Wilbur & Collins 1973). This hypothesis was supported in some studies under natural conditions (Savage 1961, Brockelmann 1969, Collins 1979, Newman 1988, 1989, Crump 1989).

First results in *H. occipitalis* indicate that larvae of this species showed a fixed very fast development (about 25 days from egg laying to metamorphosis under natural conditions) at different water level conditions that indicate a drying out of pools or improving conditions after new rain falls. Only the size at metamorphosis varies depending on the different water level conditions. But perhaps this is a result of small sample size in our study. Preliminary observations suggested that final developmental stages, from the appearance of the front limbs to the complete

resorption of the tail, are very flexible, facilitating a prolonged stay in water in the case of favourable aquatic environment.

Larvae of *B. maculatus* react to a large extent as predicted by the hypothesis of Wilbur & Collins (1973). Single tadpoles that had grown in decreasing water level conditions accelerated their development, metamorphosing smaller and faster than tadpoles that had grown in constantly high or increasing water volumes, indicating improved conditions after rainfall. Likewise, *Bufo bufo* and *Bombina variegata* that were investigated under similar conditions showed similar results (Böll et al. 1997). The best evidence for a tradeoff between development and growth in anurans was found in *Scaphiopus hammondi* (Denver et al. 1998). The control of the adaptive phenotypic plasticity is presumably carried out by hormones stimulated by different environmental cues (Denver 1997a, 1997b, 1998).

If groups of tadpoles are kept together in a single aquarium a crowding effect results, described in many studies (Brockelmann 1969, Gromko et al. 1973, Heusser & Blankenhorn 1973, Wilbur 1977a, 1977b, Collins & Cheek 1983, Newman 1987, Semlitsch 1987, Wong & Beebee 1994). If conspecific tadpoles are kept together, the larvae grow slower and metamorphose at a smaller size. Accordingly, in experiments with groups of *B. maculatus* tadpoles, the developmental time was longer and frogs at metamorphosis were smaller in comparison to experiments with single tadpoles. In treatment group HL increasing crowding effects in comparison to the HH group are to be expected. In agreement with this prediction, the frogs at metamorphosis were very small. Surprisingly, developmental time of the first metamorphosing froglet in each aquarium was shorter than in the HH-treatment group; not longer as we expected because of crowding (Spieler 1997b). Therefore, first metamorphosing froglets of each aquarium react exactly as predicted by the hypothesis of Wilbur & Collins (1973). A possible explanation is this: the crowding effect enlarged the variation in size and developmental stages of larvae within each group (Licht 1967, Gromko et al. 1973, Wilbur 1977a, Sokol 1984). At the time of changing water level in the HL group, the biggest tadpoles in each aquarium could accelerate their developmental rate at the cost of the smaller siblings and at the cost of individual growth.

One further open question is whether all anuran species show potential developmental plasticity or whether this possibility is only restricted to anurans living in – at least sometimes – unpredictable environments.

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References

- Beebee, T.J.C. (1985): Discriminate analysis of amphibian habitat determinant in South-East England. – *Amphibia-Reptilia*, Leiden 6: 35-43.
- Böll, S., M. Spieler, U. Grafe & K.E. Linsenmair (1997): Adaptations of temperate and tropical anuran larvae to the risk of desiccation and predation. – pp. 24-25 in: Third World Congress of Herpetology (eds. R. Zbyněk & H. Scott). – Durabo Celakovice, Prag.
- Bragg, A.N. (1965): Gnomes of the night: the spadefoot toads. – University of Pennsylvania press.
- Brockelmann, W.Y. (1969): An analysis of density effects and predation in *Bufo americanus* tadpoles. – *Ecology* 50: 632-644.
- Caldwell, J.P. (1989): Structure and behavior of *Hyla geographica* tadpole schools, with comments on classification of group behavior in tadpoles. – *Copeia* 1989: 938-950.
- Collins, J.P. (1979): Intrapopulation variation in the body size at metamorphosis and timing of metamorphosis in the bullfrog, *Rana catesbeiana*. – *Ecology* 60: 738-749.
- Collins, J.P. & J.E. Cheek (1983): Effect of food and density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum*. – *Amer. Zool.* 23: 77-84.
- Crump, M.L. (1989): Effect of habitat drying on developmental time and size at metamorphosis in *Hyla pseudopuma*. – *Copeia* 3: 794-797.
- Denver, R.J. (1997a): Environmental stress as a developmental cue: Corticotropin-releasing hormone is a proximate mediator of adaptive phenotypic plasticity in amphibian metamorphosis. – *Hormon. Behav.* 31: 169-179.
- Denver, R.J. (1997b): Proximate mechanisms of phenotypic plasticity in amphibian metamorphosis. – *Am. Zool.* 37: 172-184.
- Denver, R.J. (1998): Hormonal correlates of environmentally induced metamorphosis in the Western spadefoot toad, *Scaphiopus hammondi*. – *Gen. Comp. Endo.* 110: 326-336.
- Denver, R.J., N. Mirhadi & M. Phillips (1998): Adaptive plasticity in amphibian metamorphosis: Response of *Scaphiopus hammondi* tadpoles to habitat desiccation. – *Ecology* 79: 1859-1872.
- Dubois, A. (1992): Notes sur la classification des Ranidae (Amphibiens Anoures). – *Bull. mens. Soc. linn. Lyon* 61: 305-352.
- Duellman, W.E. (1993): Amphibian species of the world: additions and corrections. – *Univ. Kansas Mus. Nat. Hist., Special Publications* 21: 1-372
- Gosner, K.L. (1960): A simple table for staging anuran embryos and larvae with notes on identification. – *Herpetologica*, Lawrence, Kan. 16: 183-190.
- Gromko, M.H., F.S. Mason & S.J. Smith-Gill (1973): Analysis of the crowding effect in *Rana pipiens* tadpoles. – *J. Exp. Zool.* 186: 63-72.
- Heusser, H. & H.J. Blankenhorn (1973): Crowding – Experimente mit Kaulquappen aus homo- und heterotypischen Kreuzungen der Phänotypen

- esculenta*, *lessoneae* und *ridibunda* (*Rana esculenta*- Komplex, Anura, Amphibia). – Rev. Suisse Zool. 80: 543-569.
- Hews, D.K. (1988): Alarm response in larval western toads, *Bufo boreas*: release of larval chemicals by a natural predator and its effect on predator capture efficiency. – Anim. Behav. 36: 125-133.
- Ildas, A.S. & N. Ancona (1994): Analysis of amphibian habitat preferences in a farmland area (Po plain Italy). – Amphibia-Reptilia, Leiden 15: 307-316.
- Lamotte, M. (1967): Les batraciens de la region de Gpakobo (Côte d'Ivoire). – Bull. Inst. Fondam. Afr. Noire 19: 219-294.
- Licht, L.E. (1967): Growth inhibition in crowded tadpoles: intraspecific and interspecific Effects. – Ecology 48: 736-745.
- Linsenmair, K.E. (1998): Risk spreading and risk reducing tactics of West African anurans in an unpredictable and stressful environment. – pp. 221-241 in: Population and community dynamics in the tropics (ed. Newbery, D.M.). – Annual symposia of the British Ecological Society 1996.
- Mayhew, W.W. (1968): Biology of desert amphibians and reptiles. – pp. 196-356 in: Desert biology. (ed. G.W. Brown). – Academic Press, New York.
- Newman, R.A. (1987): Effects of density and predation on *Scaphiopus couchii* tadpoles in desert ponds. – Oecologia 71: 301-307.
- Newman, R.A. (1988): Adaptive plasticity in development of *Scaphiopus couchii* tadpoles in desert ponds. – Evolution 42: 774-783.
- Newman, R.A. (1989): Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. – Ecology 70: 1775-1787.
- Petranka, J.W. & A.G.T. Daphne (1995): Explosive breeding reduces egg and tadpole cannibalism in the wood frog, *Rana sylvatica*. – Anim. Behav. 50: 731-739.
- Poilecot, P. (1991): Un écosystème de savane soudanienne: Le Parc National de la Comoé (Côte d'Ivoire). – Paris, Organisation des Nations Unies, pour l'éducation, la science et la culture, pp 346.
- Resetarits, W.J. & H.M. Wilbur (1989): Choice of oviposition site by *Hyla chrysoscelis*: Role of predators and competitors. – Ecology, Washington 70: 220-228.
- Resetarits, W.J.J. (1996): Oviposition site choice and life history evolution. – Amer. Zool. 36: 205-215.
- Rödel, M.O. (1996): Amphibien der westafrikanischen Savanne. – Chimaira, Frankfurt.
- Rödel, M.O. & K.E. Linsenmair (1997): Predator induced swarms in the tadpoles of an African savannah frog, *Phrynomantis microps*. – Ethology 103: 902-914.
- Savage, R.M. (1961): The ecology and life history of the common frog. – Sir Isaac Putnam and Sons Ltd., London.
- Semlitsch, R.D. (1987): Paedomorphosis in *Ambystoma talpoideum*: Effects of density, food, and pond drying. – Ecology 68: 994-1002.

- Sokol, A. (1984): Plasticity in the fine timing of metamorphosis in tadpoles of the hyloid frog, *Litoria ewingi*. – *Copeia* 1984: 868-873.
- Spieler, M. (1996): Strategien der Streßvermeidung bei westafrikanischen Anuren. – *Verh. deutsch. Zool. Ges., Stuttgart*, 89: 260.
- Spieler, M. (1997a): Anpassungen ausgewählter Froschlurche an Trockenstreß und Räuberdruck in einer westafrikanischen Savanne. – *Salamandra* 33: 133-151.
- Spieler, M. (1997b): Anpassungen westafrikanischer Anuren an Austrocknungsrisiko und Räuberdruck in einem saisonalen Lebensraum. – *Wissenschaft und Technik*, Berlin, pp. 181.
- Spieler, M. (1997c): Radio-telemetrische Untersuchungen zur Laichplatzwahl eines westafrikanischen Raniden. – *Mertensiella*, Bonn 7: 203-220.
- Spieler, M. & K.E. Linsenmair (1997): Choice of optimal oviposition site by *Hoplobatrachus occipitalis* (Anura: Ranidae) in an unpredictable and patchy environment. – *Oecologia* 109: 184-199.
- Spieler, M. & K.E. Linsenmair (1998a): Biotic and abiotic factors influencing the spawning site selection of savanna anurans. – *Zoology, Supplement I*, 101: 15.
- Spieler, M. & K.E. Linsenmair (1998b): Migration patterns and diurnal use of shelter in a ranid frog of a West African savannah: a telemetric study. – *Amphibia-Reptilia* 19: 43-64.
- Spieler, M. & K.E. Linsenmair (1999): Aggregation behaviour of tadpoles of *Bufo maculatus* as an effective antipredator mechanism. – *Ethology* 105: 665-686.
- Waldman, B. (1991): Kin recognition in amphibians. – pp. 162-219 in: *Kin recognition* (ed. Hepper, P.G.). – Cambridge University Press.
- Wilbur, H.M. (1977a): Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. – *Ecology* 58: 196-200.
- Wilbur, H.M. (1977b): Interactions of food level and population density in *Rana sylvatica*. – *Ecology* 58: 206-209.
- Wilbur, H.M. & J.P. Collins (1973): Ecological aspects of amphibian metamorphosis. – *Science* 182: 1305-1314.
- Wong, A. & T. Beebee (1994): Identification of a unicellular, non-pigmented alga that mediates growth inhibition in anuran tadpoles: a new species of the genus *Prototheca* (Chlorophyceae: Chlorococcales). – *Hydrobiologica* 277: 85-96.

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Flora and vegetation of the Afromontane region in Central and East Africa

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Abstract: A survey of the Afromontane and Afroalpine vegetation is provided. The vegetation belts of Mt. Kahuzi, the Virunga volcanoes and Mt. Kenya are briefly described. Phytogeography of the East African mountains is discussed and the distribution patterns of *Dendrosenecio*, the giant *Lobelia*s and *Impatiens* within the Afromontane region are described. Some hypotheses on the origin of the Afroalpine flora are briefly discussed.

Key words: Afromontane region, Mt. Kahuzi, Virunga volcanoes, Mt. Kenya, *Dendrosenecio*, *Lobelia*, *Impatiens*

Introduction

Africa contains several isolated mountain ranges (fig.1). Their flora consists of more than 80% endemics (Hedberg 1961a). They have been called the afromontane and afroalpine archipelago-like centre of endemism (White 1983). In Central and East Africa, these mountains are situated along the Rift valley, the most important being Mt Kahuzi (3305 m a.s.l.) in eastern Congo, the eastern crest of the Central Rift valley with the Nyungwe Forest (up to 3000 m) in Rwanda, the Virunga volcanoes (4507 m) in Rwanda, Congo and Uganda, the Ruwenzori (5109 m) in Congo and Uganda, Mt Elgon (4321 m) in Uganda and Kenya, the Aberdare Mountains (3994 m) and Mt Kenya (5194 m) in Kenya, and Kilimanjaro (5895 m) and Mt Meru (4565 m) in Tanzania.

There exists a vast literature on afromontane and afroalpine flora and vegetation (e.g. Hauman 1955, Hedberg 1951, 1957, 1961a, 1965, 1969, 1986, White 1978, 1983). Several studies on single mountains have also been published (e.g. Mt Kahuzi: Fischer 1996, Hendrickx 1946, Scaetta 1934; Nyunge Forest: Fischer & Hinkel 1990, 1992, 1993, 1994, Habyaremye 1993; Virunga volcanoes: Snowden 1933; Ruwenzori: Demaret 1958, Hauman 1933, Schmitt & Beck 1992; Mt Kenya: Beck et al. 1981, Rehder et al. 1988; Aberdare Mountains: Schmitt 1991; Kilimanjaro: Klötzli 1958), but there is still a lack of vegetation analysis. The following paper intends to give an overview of the afromontane and afroalpine vegetation and their distribution patterns in Central and East Africa.

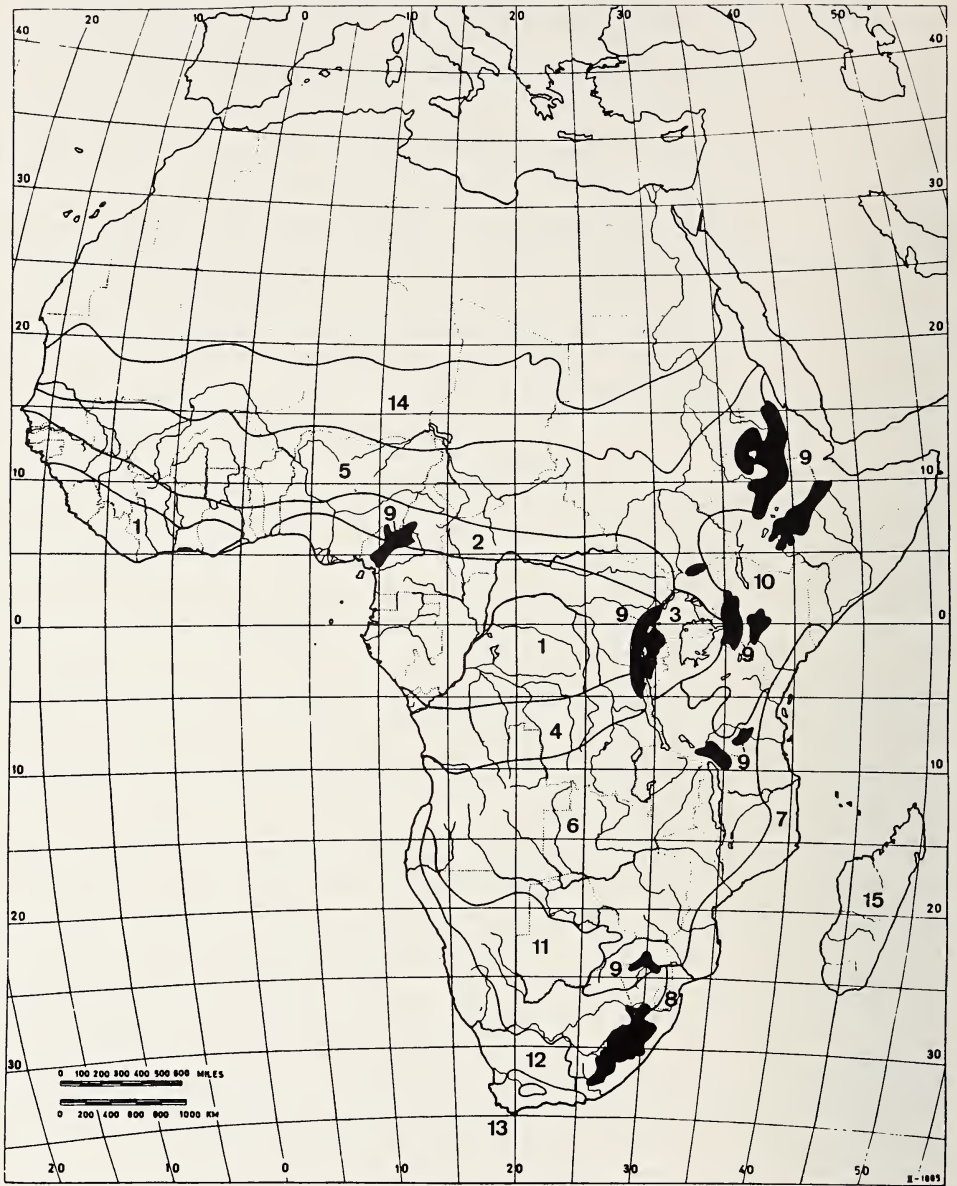


Fig.1: Main phytochoria of Africa (after White 1983): 1. Guineo-Congolian regional centre of endemism; 2. Guineo-Congolia-Sudania-Transition zone; 3. Lake Victoria regional mosaic; 4. Guineo-Congolia-Zambesia Transition zone; 5. Sudania regional centre of endemism; 6. Zambezian regional centre of endemism; 7. Zanzibar-Inhambane regional mosaic; 8. Tongoland-Pondoland regional mosaic; 9. Afromontane archipelago-like regional centre of endemism (black); 10. Somalia-Masai region; 11. Kalahari-Highveld Transition zone; 12. Karroo-Namib region; 13. Cape region; 14. Sahel Transition zone; 15. Madagascar

Altitudinal zonation

A detailed description of altitudinal zonation in East Africa was provided by Hedberg (1951). Generally, these high mountains can be divided into the western group (Mt Kahuzi, Nyungwe, Virunga volcanoes and Ruwenzori) with a much more humid climate, and the eastern mountains (Mt Elgon, Aberdares, Mt Kenya, Kilimandjaro, Mt Meru) with a considerably drier climate. Only Mt Kahuzi and Ruwenzori have a direct contact to the lowland rainforests of the Congo basin, while the other mountains are much more isolated and surrounded by savanna vegetation. The vegetation belts of the Kahuzi massif (fig.2), not mentioned by Hedberg, are briefly described here (see also Fischer 1996). From 850 m to 1300 m a.s.l. a mountain rainforest is present. There is a Transition Forest zone from 1300 to 1700 m, followed by a montane forest from 1700 to 2300 m (2400 m). From 2400 to 2600 m the bamboo zone occurs, intermixed with *Podocarpus*-forest on hill summits, swamps and in various montane forest communities. A *Hagenia-Hypericum* zone, which is well developed on the Virunga-Volcanoes, is lacking. The Ericaceous belt begins at 2600 m (Mt Biega) and reaches to 3200 m on Mt Kahuzi. The summit of Mt Kahuzi bears a *Dendrosenecio johnstoni*-Erica-subparamo and a *Helichrysum-Lobelia stuhlmannii*-paramo. In spite of the isolate position, Mt Kahuzi has several afroalpine species in common with the Virunga

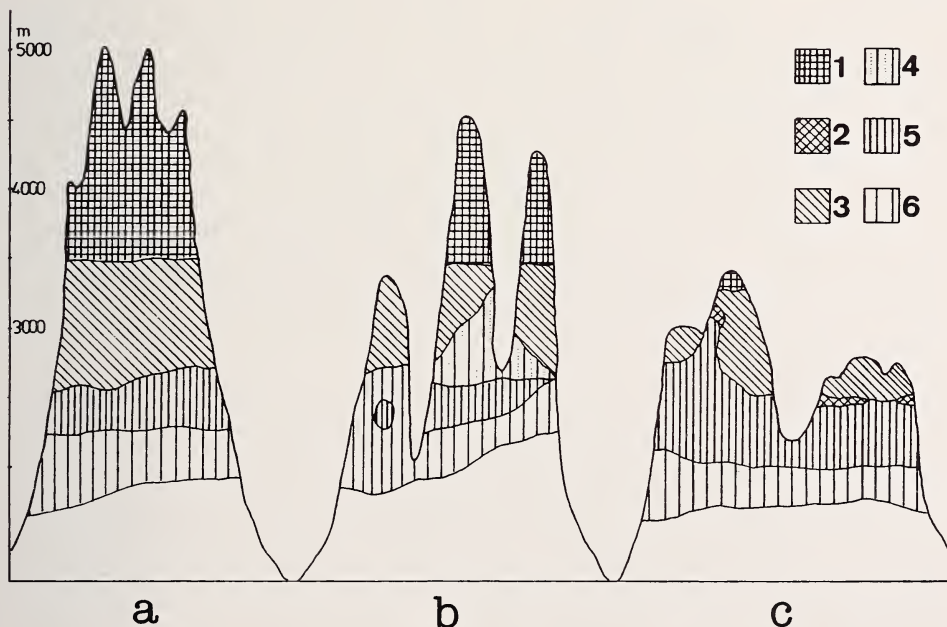


Fig.2: Altitudinal zonation of Ruwenzori (a), Virunga volcanoes (b) and Kahuzi (c) (after Fischer 1996): 1 Paramo, 2 *Podocarpus* forest, 3 Ericaceous belt, 4 *Hagenia-Hypericum* zone, 5 Bamboo zone, 6 Montane forest belt.

volcanoes and the Ruwenzori. Only *Swertia macrosepala*, *Erica johnstoni*, *Bartsia macrophylla*, *Lobelia stuhlmannii*, *Helichrysum guilelmi* and *Disa stairsii* need be mentioned. The giant groundsel *Dendrosenecio johnstoni* has proved to be a different subspecies (ssp. *kahuzicus*).

The zonation of the vegetation at the Virunga volcanoes (fig.2) is comparable. Below 2700 m, the original montane forest has been destroyed by clearcutting for agricultural purposes. From 2700 to 3000 m, a secondary *Dombeya*-montane forest

with scattered *Hagenia* has developed, followed by a *Hagenia-Hypericum* belt from 3000 to 3300 m, where large moss cushions are found. On the saddle of Karisimbi at 3400 m a moorland with *Dendrosenecio johnstoni* and *Erica johnstoni* occurs. Around Lake Muderu, a *Sphagnum* peat bog with *Carex runssorensis* has developed. Above 3400 m there is a *Dendrosenecio johnstoni-Hypericum revolutum*-subparamo. Due to acidic soil conditions, an *Erica-Philippia* forest, comparable in its floristic composition with that on Mt Kahuzi, has developed above Lake Muderu and on the steep slopes of the Susa-valley. The beginning of the paramo is at 3600 m. It can be divided into two types: the *Dendrosenecio johnstoni-Lobelia stuhlmannii*-paramo from 3600 to 3900 m, and the *Dendrosenecio johnstoni-Lobelia wollastoni*-paramo from 3900 to 4200 m. Above 4200 m no more giant groundsel are found and nearly pure meadows of *Alchemilla johnstoni* are well developed. The summit at 4507 m is covered by an alpine desert, where bryophytes and lichens dominate.

As an example of a drier eastern mountain, the vegetation belts of Mt Kenya are briefly described (see also Hedberg 1951, Rehder et al. 1988, Bussmann & Beck 1996). The montane forest belt has been divided into a lower montane forest zone from 2000 to 2700 m, the bamboo zone with dominating *Sinarundinaria alpina* from 2700 to 3200 m and the *Hagenia-Hypericum* zone from 3200 to 3400 m. This forest belt has been studied phytosociologically by Bussmann & Beck (1996). From 3400 to 3600 m, an Ericaceous belt has developed, which is considered by Rehder et al. 1988 to be part of the lower alpine zone. This Ericaceous bush is characterized by a dense cover of tussock, mainly *Carex monostachya*, which alternates with heath formations (*Erica arborea*, *Philippia keniensis*, *Stoebe kilimandscharica*). Thus it differs fundamentally from the dense Ericaceous bush on the humid western mountains. Above 3600 m, a paramo is developed, where several *Dendrosenecio* and *Lobelia* species (*D. keniodendron*, *D. keniensis*, *Lobelia telekii*, *L. deckenii* subsp. *keniensis*) are found. This alpine vegetation is also much less dense than that on the Virunga volcanoes or Ruwenzori. *Dendrosenecio keniodendron* is mainly distributed in the upper paramo up to 4400 m. The nival zone is characterized by bare soil due to the abundant solifluction and herbaceous vegetation. The rocks are densely covered with lichens most abundant among them *Alectoria sarmentosa* and *Usnea* spp.

Phytogeographical aspects

About 80% of the Afromontane and Afroalpine flora are endemic to the massifs of Central and East Africa (Hedberg 1961a). Vicarious taxa occur of different status. Some species are distributed on all or most of these mountains, like *Subularia monticola*, *Ranunculus oreophytus*, *Swertia macrosepala* or *Disa stairsii*. *Hedbergia abyssinica* is also found in the high mountains of Ethiopia, Cameroon and Malawi. In some cases, species are confined to group of mountains. A good example is the genus *Bartsia*, where *B. macrophylla* occurs on Mt Kahuzi, the Virunga volcanoes and the Ruwenzori, while *B. longiflora* and *B. decurva* are found on Mt Elgon, the Aberdares, Mt Kenya and Kilimanjaro.

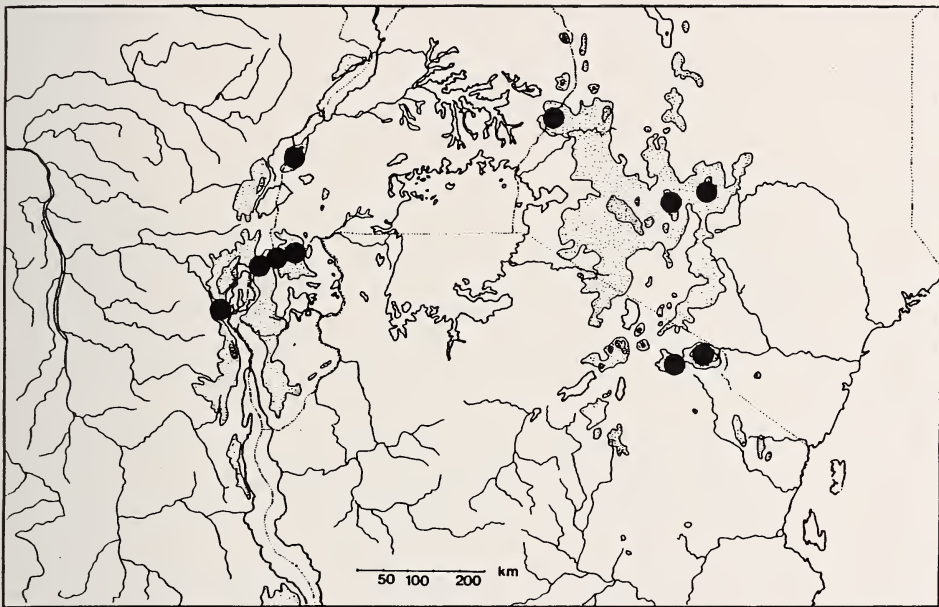


Fig.3: Distribution of *Dendrosenecio johnstoni* (after Hedberg 1986 and Mabberley 1986).

The most interesting and also most complicated genus of Afroalpine plants is *Dendrosenecio* (fig.3). Much literature exists on distribution and biology (e.g. Mildbraed 1922, Fries & Fries 1922a, Humbert 1934, Beck et al. 1982), but the taxonomy is still controversial. While Hedberg (1957, 1969) distinguished 17 species, Mabberley (1974, 1986) lumped them into four species, one of them (*D. johnstoni*) with eight subspecies. Recently, Knox (1994) argues for a narrower species concept, but more studies on ecology, morphology and molecular biology are required. Until a modern revision, the slightly modified concept of Mabberley (1986) is accepted. These taxa do not occur below 3000 m and are likely to have originated from one or two diaspores brought by long-distance dispersal. The most widespread species is *Dendrosenecio johnstoni* (fig.3). *D. johnstoni* subsp. *kahuzicus* is endemic on Mt Kahuzi, subsp. *adnivalis* occurs on the Virunga

volcanoes and Ruwenzori, while the var. *friesiorum* is endemic to Ruwenzori. *Dendrosenecio johnstoni* subsp. *cheranganiensis* and subsp. *dalei* are both endemics on the Cherangani Hills in Kenya, the subsp. *elgonensis* and subsp. *barbatipes* are confined to Mt Elgon, and subsp. *battiscombei* is restricted to Mt Kenya and the Aberdare Mountains. On Kilimanjaro subsp. *cottonii* and subsp. *johnstoni* are found, the latter being present also on Mt Meru. Mt Kenya harbours two endemic species, *Dendrosenecio keniodendron* and *D. keniensis* (= *Senecio brassica*). One species, *D. brassiciformis*, is confined to the Aberdare Mountains.

A similar picture is provided by the giant lobelias (Fries & Fries 1922b, Hedberg 1957, Thulin 1984). *Lobelia deckenii*, with its vicarious subspecies, is a good example of a rapid genetic drift, which originated in differences in splitting of corolla and pubescence of bracts, sepals, petals and anthers (Hedberg 1969). *L. deckenii* subsp. *deckenii* is endemic on Kilimanjaro, subsp. *elgonensis* on Mt Elgon, subsp. *keniensis* on Mt Kenya, subsp. *sattimae* on the Aberdare Mountains, and subsp. *burtii* on Mt Meru and the Ngorongoro crater. *Lobelia deckenii* subsp. *bequaertii* is the westernmost taxon of this group and confined to the Ruwenzori. Other *Lobelia* species are found on several mountain systems, but no differentiation into subspecies can be observed. *Lobelia wollastonii* is endemic to the Virunga volcanoes and the Ruwenzori, while its vicarious species *L. telekii* is restricted to Mt Elgon, Mt Kenya and the Aberdare Mountains. The closely related *L. stuhlmannii* is found on Mt Kahuzi, the Virunga volcanoes and Ruwenzori. Other vicarious species pairs are *Lobelia bambuseti* on Mt Kenya and Aberdare Mountains and *L. petiolata* on Mt Kahuzi and the Virunga volcanoes, as well as *L. aberdarica* on Mt Elgon, Mt Kenya, and the Aberdare Mountains and *L. mildbraedii* on Mt Kahuzi, the Virunga volcanoes, the Congo-Nile watershed and Ruwenzori.

Finally, the distribution of several *Impatiens* species (Grey-Wilson 1980) can be regarded as a model system. The *Impatiens filicornu* aggregate is represented on Mt Kahuzi, the Congo-Nile watershed, the Virunga volcanoes and Ruwenzori with *Impatiens bequaerti*, *I. mildbraedii* subsp. *mildbraedii*, *I. erecticornis* and *I. purpureo-violacea*. The closest relative, *Impatiens mildbraedii* subsp. *telekii* is restricted to Mt Kenya and the Aberdare Mountains. The *Impatiens stuhlmannii* aggregate, with *I. apiculata*, *I. masisiensis* and *I. warburgiana*, is endemic to the western group (Mt Kahuzi, the Congo-Nile watershed, the Virunga volcanoes, Ruwenzori) and only *I. stuhlmannii* is also found on Mt Elgon. Of the *Impatiens tinctoria* aggregate, only *I. tinctoria* subsp. *tinctoria* is found on Ruwenzori, while *I. tinctoria* subsp. *elegantissima* is endemic to Mt Elgon, Mt Kenya and the Aberdares. *Impatiens fischeri* is restricted to Mt Kenya and the Aberdare Mountains. The western humid mountains are apparently a centre of endemism for *Impatiens*. The *Impatiens kilimanjari* aggregate is represented here by *Impatiens runssorensis* (Ruwenzori), *I. bururiensis*, *I. gesneroidea*, *I. quadrisepala* (Congo-Nile watershed) and *I. superglabra* (Mt Kahuzi), while *I. kilimanjari* is endemic to Kilimanjaro. *Impatiens keilii* and *I. paucidentata* from the *Impatiens gomphophylla* aggregate are also restricted to the Congo-Nile watershed in the Central Rift Valley. On Mt Elgon, the following taxa of this group are endemic: *Impatiens tweediae*, *I. miniata* and *I. digitata* subsp. *phlyctidoceras*. *Impatiens digitata* subsp. *digitata* is confined to Kilimanjaro. The *Impatiens rubromaculata* aggregate is

found only on the eastern mountains. *Impatiens hoehnelii* and *I. meruensis* subsp. *cruciata* are endemic on Mt Kenya and Aberdares, while *I. meruensis* subsp. *meruensis*, *I. rubromaculata* subsp. *rubromaculata* and *I. nana* are found only on Kilimanjaro. These distribution patterns may be explained by long-distance dispersal and sub-sequent radiation of a taxon. However, we also have to consider the refugial hypothesis of Hamilton (1974, 1982). There is strong evidence (Bonne-

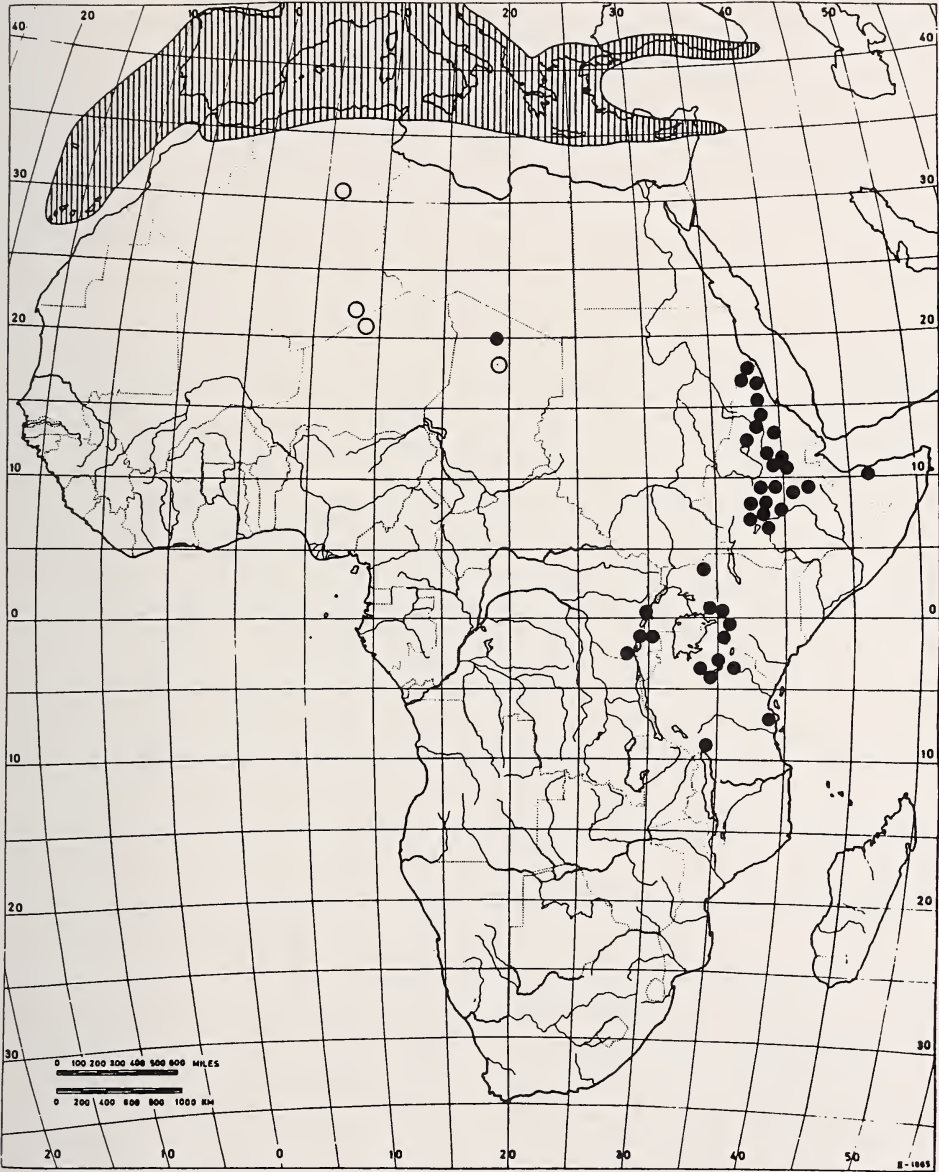


Fig.4: Distribution of *Erica arborea* (after Fischer 1996). Closed distribution area hatched, subfossil records (open circles).

fille et al. 1990, Grunderbeek et al. 1983) that during the last glacial period (18 000 B.P.) the climate in Africa was cool and dry, resulting in a lowering of the vegetation belts and a forest decline. Humid forests survived only in particular



Fig.5: Distribution of *Canarina eminii* (circles) and *C. canariensis* (stars) (after Hedberg 1961b).

refugial areas (see also Fischer 1996) and the distribution pattern of some Afromontane species perfectly reflects these refugia. The origin of the Afromontane flora by migrating taxa during the Tertiary period is supported by an interesting phytogeographical link between Macaronesia and East Africa (Lösch & Fischer 1994). Here, in the Ericaceous shrub vegetation, numerous vicarious taxa could be demonstrated, among them *Erica arborea* (fig.4) which is present in Macaronesia, the Mediterranean region and the East African mountains as well. Stepping-stones can be found in the Saharan region by subfossil records and even a recent locality. Another example for vicarious taxa is provided by the genus *Canarina* (Hedberg 1961b) (fig.5), where *C. canariensis* is endemic to the Canary islands and *C. eminii* and *C. abyssinica* are East African species. Also the genus *Dendrosenecio* and the giant *Lobelias* may have originated during the Tertiary. As pointed out above, a long distance dispersal between isolated mountains and subsequent radiation might have been important for the evolution of the afromontane flora.

References

- Beck, E., H. Rehder, P. Pongratz & M. Senser (1981): Ecological analysis of the boundary between afroalpine vegetation types “*Dendrosenecio* woodlands” and “*Senecio brassica-Lobelia keniensis* community” on Mt Kenya. – J. East African Nat. Hist. Soc. and Nat. Mus. 172: 11 p.
- Beck, E., M. Senser, R. Scheibe, H.M. Steiger & P. Pongratz (1982): Frost avoidance and freezing tolerance in Afroalpine “giant rosette” plants. – Plant Cell & Environm. 5: 215-222.
- Bonnefille, R., J.C. Roeland & J. Guiot (1990): Temperature and rainfall estimates for the past 40,000 years in equatorial Africa. – Nature 346: 347-349.
- Bussmann, R.W. & E. Beck (1996): The forests of Mount Kenya – A phytosociological synopsis. – Phytocoenologia 25: 467-560.
- Demaret, F. (1958): Aperçu sur la flore et la végétation des forêts à *Hagenia abyssinica* (Bruce) Gmel. du Ruwenzori occidental. – Bull. Jard. Bot. Brux. 28: 331-337.
- Fischer, E. (1996): Die Vegetation des Parc National Kahuzi-Biéga/Zaire. – Erdwiss. Forschung 35: 1-240.
- Fischer, E. & H. Hinkel (1990): Untersuchungen zur Einnischung der Herpetofauna in Nebelwäldern Ruandas (Zentralafrika). – Mainzer Geowiss. Studien 34: 485-502.
- Fischer, E. & H. Hinkel (1992): Natur Ruandas, La nature au Rwanda. Einführung in die Flora und Fauna Ruandas, Aperçu sur la flore et la faune rwandaise. Materialien zur Partnerschaft Rheinland-Pfalz/Ruanda, 1992/1. – Rhein-Main-Verlagsgruppe, Mainz.
- Fischer, E. & H. Hinkel (1993): Zur Flora und Fauna der Wälder Ruandas/Zentralafrika. I. Der Cyamudongo-Wald. – Mainzer Naturwiss. Archiv 31: 239-275.

- Fischer, E. & H. Hinkel (1994): Zur Flora und Fauna der Wälder Ruandas/ Zentralafrika. II. Der Gishwati-Wald. – Mainzer Naturwiss. Archiv 32: 39-85.
- Fries, R.E. & T.C.E. Fries (1922a): Über die Riesen-Senecionen der afrikanischen Hochgebirge. – Svensk. Bot. Tidskr. 16: 321-340.
- Fries, R.E. & T.C.E. Fries (1922b): Die Riesen-Lobelien Afrikas. – Svensk. Bot. Tidskr. 16: 383-416.
- Grey-Wilson, C. (1980): Impatiens of Africa. – A.A. Balkema, Rotterdam.
- Grunderbeek, M.C. van, E. Roche & H. Doutre-Lepont (1983): Le premier Age du Fer au Rwanda et au Burundi, archéologie et environnement. – I.N.R.S. Butare – Rwanda, Publication 23: 1-57.
- Habyaremye, F.X. (1993): Analyse Phytosociologique des Forêts Primaires de la Crête Zaire-Nil au Rwanda. – Belg. Journ. Bot. 126: 100-134.
- Hamilton, A.C. (1974): Distribution patterns of forest trees in Uganda and their historical significance. – Vegetatio 29: 21-35.
- Hamilton, A.C. (1982): Environmental history of East Africa. – Academic Press.
- Hauman, L. (1933): Esquisse de la végétation des hautes altitudes sur le Ruwenzori. – Bull. Acad. roy. Belg. (Classe des Sciences), 5e série 19: 602-616, 702-717, 900-917.
- Hauman, L. (1955): La “Région afroalpine” en phytogéographie centro-africaine. – Webbia 11: 467-469.
- Hedberg, O. (1951): Vegetation belts of the East African mountains. – Svensk Bot. Tidskr. 45: 140-202.
- Hedberg, O. (1957): Afroalpine vascular plants. A taxonomic revision. Symbolae Bot. Upsalienses 15, 1: 1-411.
- Hedberg, O. (1961a): The phytogeographical position of the afroalpine flora. – Recent Advances Bot. 1: 914-919.
- Hedberg, O. (1961b): Monograph of the genus *Canarina* L. (Campanulaceae). – Svensk Bot. Tidskr. 55: 17-62.
- Hedberg, O. (1965): Afroalpine flora elements. – Webbia 19: 519-529.
- Hedberg, O. (1969): Evolution and speciation in a tropical high mountain flora. – Biol. J. Linn. Soc. 1: 135-149.
- Hedberg, O. (1986): Origins of the afroalpine flora. – pp. 444-468 in: High altitude tropical biogeography (eds. Vuilleumier, F. & M. Monasterio.) – Oxford University Press.
- Hendrickx, F.L. (1946): Esquisse de la végétation du Kahusi. – Rev. Agron. col., Bukavu, 3e trim. 1946, 25-32.
- Humbert, H. (1934): Sur un Senecio arborescent nouveau des hautes montagnes du Congo belge et sur les liens phylogénétiques des espèces alliées. – Bull. Soc. Bot. 81: 830-848.
- Klötzli, F. (1958): Zur Pflanzensoziologie des Südhangs der alpinen Stufe des Kilimandscharo. – Ber. Geobot. Inst. Rübel 1957: 33-59.

- Knox, E. (1994): Species concepts in the giant Lobelias and the giant Senecios. – Proc. XIIIth Plenary Meeting AETFAT, Malawi 1: 467-471.
- Lösch, R. & E. Fischer (1994): Vikariierende Heidebuschwälder und ihre Kontaktgesellschaften in Makaronesien und Zentralafrika. – Phytocoenologia 24: 695-720.
- Mabberley, D.J. (1974): Evolution of the giant groundsels. – Kew Bull. 28 (1): 61-96.
- Mabberley, D.J. (1986): Adaptive syndromes of the afroalpine species of *Dendrosenecio*. – pp. 81-102 in: High altitude tropical biogeography (eds. Vuilleumier, F. & M. Monasterio.) – Oxford University Press.
- Mildbraed, J. (1922): Zur Kenntnis der *Senecio*-Bäume der afrikanischen Hochgebirge. – Feddes Rept. 18: 227-232.
- Rehder, H., E. Beck & J.O. Kokwaro (1988): The afroalpine plant communities of Mt Kenya (Kenya). – Phytocoenologia 16: 433-463.
- Scaetta, H. (1934): Le climat écologique de la dorsale Congo-Nil (Afrique centrale équato-riale). – Inst. Roy. Col. Belge, Sect. Sc. Nat. Méd., Mém. 4°, 3. Bruxelles.
- Schmitt, K. (1991): The Vegetation of the Aberdare National Park, Kenya. – Hochgebirgsforschung 8: 1-259. Innsbruck.
- Schmitt, K. & E. Beck (1992) On the afroalpine vegetation of the Ruwenzori Mountains, Uganda. – Phytocoenologia 21: 313-332.
- Snowden, J.D. (1933): A study in altitudinal zonation in South Kigezi and on Mounts Muhavura and Mgahinga. – Uganda. J. Ecol. 21: 7-27.
- Thulin, M. (1984): Lobeliaceae. – pp. 1-59 in: Flora of Tropical East Africa (ed. Polhill, R.M.). – A.A. Balkema, Rotterdam.
- White, F. (1978): The Afromontane Region. – pp. 463-513 in: Biogeography and ecology of Southern Africa (ed. Werger, M.J.A.). – Junk, The Hague.
- White, F. (1983): The vegetation of Africa. A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. – Paris.

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Systematics and distribution patterns of Afrotropical Canaries (*Serinus* species group, Aves, Passeriformes, Carduelidae)

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Abstract: A brief comparison of results obtained from a morphological and a molecular approach to canary phylogeny is given. Based on the molecular hypothesis, distribution patterns of species under study in both analyses are reevaluated. In molecular trees, nodes of high bootstrap values in stable clusters support monophyletic species groups also found in the morphological dataset. The respective species show mostly allopatric distribution, similar gross habitat demands and are of younger phylogenetic age than species clustered at deep nodes and/or with low bootstrap values. Distribution patterns of these species are either disjunct or sympatric, and gross habitat demands differ.

Key words: systematics, distribution patterns, Carduelidae, Afrotropis

Introduction

Carduelidae is a family of songbirds spread almost worldwide. It comprises about 140 species, of which 32 (Paynter 1968) to 45 taxa (Sibley & Monroe 1990) are placed within the genus *Serinus* Koch, 1816. Distribution of these species is focussed, with 38 members, in the Afrotropis. Two species of the Afrotropical stock also inhabit the Arabian Peninsula, five occur in the Palaearctic and two in the Oriental Regions. In two recent papers, rapid radiation (Arnaiz-Villena et al. 1999) and systematics and distribution patterns (van den Elzen & Khoury 1999) of this species group were analyzed, using two different methods, a molecular (Arnaiz-Villena et al. 1999) and a combined morphological-ethological approach (van den Elzen & Khoury 1999). As the two studies correspond in some of their results and complement each other, both analyses are summarized here, a short comparison is given and, based on the molecular hypothesis of canary phylogeny, distribution patterns of species under study in both analyses are reevaluated.

Phylogenetic analyses

Results of the morphological approach

In the systematical analysis, 5 ethological and 6 morphological characters found as synapomorphies in 23 extant canary species were polarized from two outgroups *Fringilla coelebs* and *Chloris chloris* and *P. striolata* and *C. thibetana* (see table 1, details in van den Elzen & Khoury 1999). A first-hand cladogram of all 25 species obtained 5 species groups (see also van den Elzen 1985), later given generic rank, mainly following the nomenclature of Wolters (1979): *Serinus* (sensu stricto, 5 species: *alario*, *citrinella*, *canicollis*, *syriacus*, *pusillus* within this study),

Table 1: Behaviour and plumage patterns of *Serinus* species used for cladistic analysis (nomenclature follows Wolters 1979).

Genus	species	01	02	03	04	05	06	07	08	09	10	11
<i>Fringilla</i>	<i>coelebs</i> /juv	?	0	0	0	0	1	0	0	0	1	0
<i>Chloris</i>	<i>chloris</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Alario</i>	<i>alario</i>	0	0	0	0	1	0	2	2	1	1	0
<i>Serinus</i>	<i>citrinella</i>	0	0	0	0	1	1	0	0	1	1	0
<i>Serinus</i>	<i>canicollis</i>	0	0	0	0	1	1	0	0	1	1	0
<i>Serinus</i>	<i>syriacus</i>	0	0	0	0	1	1	0	0	1	1	0
<i>Serinus</i>	<i>pusillus</i>	0	0	0	0	1	1	2	2	1	1	0
<i>Serinus</i>		0	0	0	0	1	1	0	0	1	1	0
<i>Crithagra</i>	<i>leucoptera</i>	?	1	1	0	1	0	0	2	3	?	1
<i>Crithagra</i>	<i>striolata</i>	1	1	1	0	1	0	1	1	3	0	1
<i>Crithagra</i>	<i>gularis</i>	1	1	1	0	1	0	0	2	3	1	1
<i>Crithagra</i>	<i>tristriata</i>	1	1	1	0	1	0	2	2	3	1	1
<i>Poliospiza</i>		1	1	1	0	1	0	?	2	3	1	1
<i>Dendrospiza</i>	<i>citrinelloides</i>	1	0	1	0	1	0	2	2	2	0	1
<i>Dendrospiza</i>	<i>hyposticta</i>	1	0	1	0	1	0	2	2	2	0	1
<i>Dendrospiza</i>	<i>scotops</i>	1	0	1	0	1	0	2	2	2	0	1
<i>Dendrospiza</i>		1	0	1	0	1	0	2	2	2	0	1
<i>Serinops</i>	<i>flaviventris</i>	1	1	2	0	0	1	1	1	1	0	1
<i>Crithagra</i>	<i>sulphurata</i>	1	1	2	0	0	0	1	1	1	0	1
<i>Crithagra</i>	<i>donaldsoni</i>	1	1	2	0	0	1	1	1	1	0	1
<i>Crithagra</i>	<i>albogularis</i>	1	1	2	0	0	1	1	1	3	0	1
<i>Crithagra</i>		1	1	2	0	0	1	1	1	1	0	1
<i>Ochrospiza</i>	<i>leucopygia</i>	1	1	3	1	1	0	0	0	0	0	1
<i>Ochrospiza</i>	<i>reichenowi</i>	1	1	3	1	1	1	1	1	3	0	1
<i>Ochrospiza</i>	<i>atrogularis</i>	1	1	3	1	1	1	1	1	3	0	1
<i>Ochrospiza</i>	<i>citrinipectus</i>	1	1	3	1	1	1	1	1	3	0	1
<i>Ochrospiza</i>	<i>mozambica</i>	1	1	3	1	1	1	1	1	1	0	1
<i>Ochrospiza</i>	<i>dorsostrciata</i>	1	1	3	1	1	1	1	1	1	0	1
<i>Ochrospiza</i>	<i>xanthopygia</i>	1	1	3	1	1	1	0	1	3	0	1
<i>Ochrospiza</i>		1	1	3	1	1	1	1	1	?	0	1

Characters 01-11

01 attraction call of juveniles: 0= identical to begging calls, short, no frequency modulations; 1= frequency modulated, of long duration

02 Head-up posture (aggressive display): 0= wings spread; 1= head-up posture

03 courtship display: 0= lateral displaying, pivoting; 1= fluffed display, 2= head-up posture, 3= heraldic-eagle display

04 nestbuilding: 0= by ♀ only, 1= also by ♂

05 transport of nesting materials: 0= by ♀ only, 1= also by ♂

06 rump coloration: 0= as colour of back; 1= contrasting

07 ear patch: 0= weak; 1= prominent, contrasting; 2= non-existent

08 moustachial stripe: 0= weak; 1= dark and contrasting; 2= non-existent

09 head pattern: 0= uniform, no supercilium; 1= yellow supercilium; 2= s. black and yellow; 3= s. white

10 juvenile plumage: 0= as adult pl.; 1= different to ad. pl.

11 gape coloration of nestlings: 0= red; 1= blue patches on red

0 = plesiomorphic condition, 1(2,3 in transformation series) = apomorphic conditions, ? = no information

Ochrospiza (7 species: *leucopygia*, *reichenowi*, *atrogularis*, *citrinipectus*, *mozambica*, *dorsostrata*, *xanthopygia*), *Crithagra* (4 species: *flaviventris*, *sulphurata*, *donaldsoni*, *albogularis*), *Poliospiza* (4 species: *leucoptera*, *striolata*, *gularis*, *tristriata*) and *Dendrospiza* (3 species: *citrinelloides*, *hyposticta*, *scotops*).

As relationships between genera were still unsolved, the dataset was analyzed with the computer programme HENNIG 86. Six trees were found but are not taken into consideration, as they have only poor solutions and low tree stability with a consistency index of 51. Tree stability in computer-based phylogenetic analyses needs a support of 5 characters per node (Mooers et al. 1995), not given in the dataset of van den Elzen & Khoury (1999) as species outnumbered characters by 25 to 11. Lacking additional clear synapomorphies, the number of taxa was reduced by summarizing characters of species groups supported in the first analysis. Thus only 7 taxa represented 5 canary species groups (genera *Serinus*, *Ochrospiza*, *Crithagra*, *Poliospiza* and *Dendrospiza*) plus the two outgroups (table 1, generic names and details in: van den Elzen & Khoury 1999).

Despite the fact that 11 characters had to support 6 nodes, the HENNIG 86 analyses provided one single tree of rather good quality (21 steps, consistency index 80, retention index 80). It places (fig.1) the *Serinus* species next to the outgroups *Fringilla* and *Chloris* at the base of the tree. Thus *Serinus* is the (phylogenetically older) sister taxon of a monophyletic entity comprising four taxa in two sister groups: *Ochrospiza* plus *Crithagra* on the one hand, *Poliospiza* with *Dendrospiza* on the other.

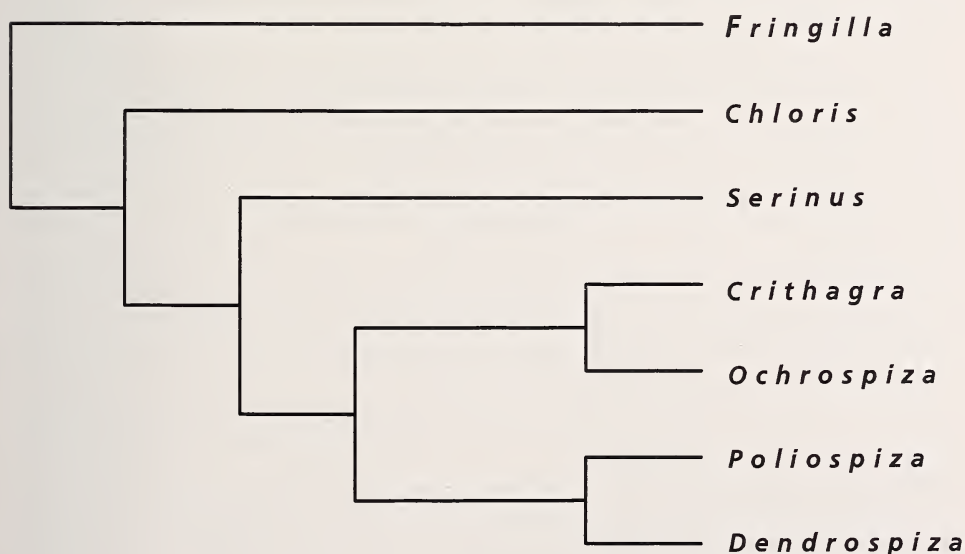


Fig.1: HENNIG 86-tree from behavioural and morphological characters of species groups mediated under generic names given in table 1.

Results of the molecular analysis

Arnaiz-Villena et al. (1999) studied 18 (17, if *S. canicollis flavivertex* is treated as a subspecies) “*Serinus*” species using mitochondrial DNA of the cytochrome b gene. Their sample comprises, in the nomenclature put forward in van den Elzen & Khoury (1999), the following species: *Serinus alario*, *S. canaria* (wild birds and domesticated form), *S. serinus*, *S. canicollis* (in two populations *S. c. canicollis* and *S. c. flavivertex*); *Ochrospiza atrogularis*, *O. leucopygia*, *O. citrinipectus*, *O. dorsostriata*, *O. mozambica*; *Crithagra flaviventris*, *C. sulphurata*, *C. albogularis*; *Poliospiza gularis*, *P. striolata*; *Chionomitris thibetana*. As outgroups, DNA sequences of *Fringilla coelebs* and *Passer luteus* were compared, as well as two non-passerine galliform species: *Lophura nycthemera* and *Gallus gallus*. The authors present three dendrograms obtained by three different mathematical procedures (algorithms): unweighted maximum parsimony heuristic search (PAUP), neighbour-joining bootstrap and UPGMA.

In their parsimony and neighbour-joining trees Arnaiz-Villena et al. (1999) show bootstrap values above 50, found in 15 of 20 nodes in the parsimony analysis and 14 of 20 nodes in the neighbour-joining tree. High bootstrap (80 and above) supports nodes and thus phylogenetic relationships of the following species and species-groups in both dendrograms: *Fringilla* as an outgroup to the Carduelidae under study (fig.2: node A); *canaria* and *serinus* (fig.2: cluster D, node 4), *alario* and *canicollis* (fig.2: cluster D, node 3), *flaviventris* and *sulphurata* (fig.2: cluster C, node 2), *atrogularis* and *leucopygia* (fig.2: cluster C, node 1), as sister taxa. Neighbour-joining defended a clade *alario-canicollis-pusillus* (fig.2: D, 3a) and another consisting of *atrogularis-leucopygia-citrinipectus-dorsostriata* (Fig.2: C, 1b). Not shown in fig.2 are the relationships of domesticated and wild *Serinus canaria* (bootstrap 100) and of *Serinus canicollis flavivertex* to nominate *canicollis* (bootstrap 98).

Within all three dendrograms three species-groups were placed concordantly.

- One node (fig.2, D) postulates phylogenetic relationships of species within two subclusters: *canaria-serinus* and *alario-canicollis-pusillus*, and thus supports the morphological-ethological findings and species limits of the restricted genus *Serinus* proposed by van den Elzen & Khoury (1999).
- A second node (fig.2, C, b) places *atrogularis-leucopygia-citrinipectus-dorsostriata* into one cluster that includes not only *mozambica* but also *citrinelloides*, from a different monophyletic unit, the *Dendrospiza*-species group, as depicted in two dendrograms, parsimony and neighbour-joining, but not the UPGMA (see above). A monophylogenetic relationship of only 5 of these 6 taxa (as members of the genus *Ochrospiza*) was suggested by van den Elzen & Khoury (1999), but the two genera *Ochrospiza* and *Dendrospiza* proved not to be closely related (fig.1). Thus the hypothesis that *Ochrospiza* species are a monophyletic entity is only partly supported.
- A third invariable node (fig.2: C, c) groups four species: *flaviventris*, *sulphurata*, *albogularis*, *gularis*. It also does not support a closer relationship of *Crithagra* species within the limits of the morphological analysis as it places *gularis* into a distinct species group, genus *Poliospiza*. The three tree topologies of the DNA

analysis also do not sustain a broad genus *Crithagra* (sensu Wolters 1979, lumping *Poliospiza* and *Crithagra* species), as they place *P. striolata* either next to *C. thibetana* (fig.2, B, a), and their common node (fig.2, B) in a sister group position to the *Serinus* s.str. node (parsimony tree) or to the node of the Afrotropical clade (neighbour-joining tree, fig.2), or both taxa separately in an outgroup position to the first node of the other 15 species of the whole sample (UPGMA tree).

Of the five lineages proposed by van den Elzen & Khoury (1999), none is unquestionably verified by the mtDNA study. *Serinus* and *Ochrospiza* are partly supported, whereas *Poliospiza* appears to be paraphyletic and the species limits of *Crithagra* may have to be reevaluated. The choice of only one single representative of the *Dendrospiza* species group, *D. citrinelloides*, may have disturbed the tree topology as indicated by the low bootstrap values of 53 and below.

Phylogenetic relationships between the three monophyletic entities described above could not be proved by the molecular analysis. *Serinus* s.str. appears in the three trees figured by Arnaiz-Villena et al. (1999) as the sister taxon to either the Afrotropical clade of van den Elzen & Khoury (1999) (genera *Ochrospiza*, *Crithagra*, *Poliospiza*, *Dendrospiza*; neighbour-joining tree), the *P. striolata*-*C. thibetana* node (parsimony tree), or the *flaviventris-sulphurata-albogularis-gularis* node (UPGMA tree). In the latter, the *canaria-serinus* node is joined by *mozambica* and *citrinelloides* as sister taxa, with the cluster *alario-canicollis-pusillus* in a stable sister-group position.

The parsimony tree depicts a common node of *Serinus* s.str. (including *P. striolata* and *C. thibetana* with bootstrap values below 50) with *Ochrospiza* (including *mozambica*), and with “*Crithagra*” as their sister taxon. The neighbour-joining tree sketches a *Serinus* s.str. cluster opposing a cluster formed by three subgroups, one including the complete sample of *Ochrospiza* species plus *mozambica*, another the “*Crithagra*” subgroup with the already mentioned restriction of *P. striolata*, which forms, combined with *C. thibetana*, the third subset. In the UPGMA dendrogram, *Serinus* species are disrupted by *O. mozambica* and *D. citrinelloides*. Their sister taxon is the mixed *Crithagra*-*Poliospiza* *gularis* group, and both clusters have *Ochrospiza* species (solely *O. mozambica*) as a sister taxon, opposed by *P. striolata* and *C. thibetana*.

The UPGMA tree in Arnaiz-Villena et al. (1999) also gives an approximate time calculation calibrated on the known divergence time of *Lophura nycthemera* and *Gallus gallus*, 19 Mya. Based on this assumption, *C. thibetana* appears as the phylogenetically most distant and thus oldest species in the sample, diverging about 9 Mya, *Ochrospiza* species are relatively older than the other Afrotropical species under discussion, while the true canaries *Serinus* s.str. are the youngest clade.

Analyses of distribution patterns

According to the vicariance model of Nelson & Platnick (1981), phylogeny can be inferred from distribution patterns. Speciation is assumed to proceed in geographical isolation, a partial requirement also of the Biological Species Concept (Mayr 1942, 1992). Vicariants are allopatric in their distribution and have similar ecological demands. Therefore species ranges of sister taxa, or of a proposed

monophyletic species group, should be allopatric in early stages of differentiation. It can also be expected that phylogenetically younger species have roughly similar ecological demands and are to be found in more similar habitats than phylogenetically older species but in different niches, as postulated in the extended species concept (Mayr 1992).

Distribution patterns were presented by van den Elzen & Khoury (1999) on counts of species occurrence in 5° x 5° grids. The main sources were the distribution maps in Hall & Moreau (1970), supplemented by individual maps in Ash & Miskell (1998), Clemetn et al. (1993), Gatter (1997), Harrison et al. (1997), Lewis & Pomeroy (1989) and Irwin (1964).

Centres of diversity of Afrotropical "*Serinus*" s.lat. (38 species in Sibley & Monroe 1990) are montane habitats of the Albertine Rift Mountains where 12 species occur. Three minor centres with 8 species each are in the Angolan, east Zimbabwean and Eastern Arc Mountains. West Arica is poorest, with a species maximum of 3 and an average of 1.7 within 5° grids, montane areas in East Africa, with an average of 7.4 species per square, are richest in canary species abundance. Counted by altitudinal distribution, lowland species outnumber montane taxa: 21 versus 15. Two species (*S. canicollis* and *Dendrospiza scotops*) are occurring in both habitats (details in van den Elzen & Khoury 1999).

The four species groups which were separated as the genera *Crithagra*, *Ochrospiza*, *Poliospiza* and *Dendrospiza* from *Serinus* s.lat. are genuine Afrotropical inhabitants. Most species of the genus *Serinus* s.str. breed in restricted ranges around the Mediterranean basin, *Serinus pusillus* occurs from Turkey into the Himalayas, whereas *Serinus canicollis* and *Serinus (Alario) alario* inhabit the Afrotropical region. The two species used as outgroups in the HENNIG 86 analysis, *Fringilla coelebs* and *Chloris chloris*, are distributed in the Palearctic region. *Fringilla* reaches the African continent and has breeding populations in the Canary Islands and parts of North Africa. *Chloris chloris* has its nearest relatives in the Himalayas.

Within the Afrotropical endemic genera, species ranges were found to be allopatric to parapatric in most cases or, if sympatric, species are separated by diverging ecological requirements (details in van den Elzen & Khoury 1999). Centres of species diversity for *Poliospiza* and *Dendrospiza* are montane in the northeastern Rift Valley, for *Crithagra* montane to lowland areas in southern Africa, and for *Ochrospiza* lowlands in northeastern Africa. A topographical divergence of lineages, that is adaptation of species of any of the proposed genera to either montane or lowland habitats, could not be confirmed. As each has representatives in both environments, genera can only be characterized by their distribution centres. As indicated by the ranges of different *Serinus canicollis*-populations – reaching from high altitude montane areas in East Africa to man-made environments in southern Africa – landscape requirements are seemingly not key factors for habitat choice of the species.

As large-scale investigations have shown, distribution patterns are known to correspond best to climatic factors (O'Brien 1998). Van den Elzen & Khoury (1999) explained canary distribution ranges and patterns by climate and climatic changes in the past leading to habitat fluctuations and shifts. The geographic posi-

Table 2: Nodes from the neighbour-joining tree of Amaiz-Villena et al. (1999; fig. 1b) and their interpretation. N.s.= not shown, bootstrap lower than 50; allopatric= allopatric distribution of species clustered by the node, parapatric= parapatric distribution of species, symp.= sympatric distribution; EK coincidence=nodes also confirmed by van den Elzen & Khoury (1999); ntaxa= number of taxa clustered by node; taxa relations= number of taxa per sister group; taxa concerned= taxa clustered belong to different: family= families, genera= to different genera, genus= different species of one genus (limits of van den Elzen & Khoury 1999); n.p.= node not presented in the time calculation tree of A-V. (6+) phylogenetic age judged from different node.

Node	A	B	C	D	a	b	c	1c	1b	1a	2a	3a	1	2	3	4
bootstrap	100	100	n.s.	65	n.s.	n.s.	63	n.s.	80	56	50	89	82	100	96	98
tree stability	no	no	no	yes	partl	no	yes	no	yes	yes	yes	yes	yes	yes	yes	yes
distribution	allopatric	symp.	symp.	parapatric	allopatric	symp.	symp.	allopatric	allopatric	allopatric	symp.	allopatric	allopatric	parapatric	allopatric	allopatric
habitat	different	different	different	different	unknown	similar	different	different	similar	similar	different	similar	similar	similar	sim/diff	similar
EK coincidence	yes	no	no	yes	no	no	no	no	yes	yes	no	yes	yes	yes	yes	yes
ntaxa / taxa relations	18 5/12	12 2/10	10 6/4	5 3/2	2	6 1/5	4 1/3	5 1/4	4 1/3	3 1/2	3 1/2	3 1/2	2	2	2	2
taxa concerned	family	genera	genera	genera	genera	genera	genera	genera	genera	genera	genera	genus	Sspec	Sspec	Sspec	Sspec
phylogenetic age	17 mya	n.p.	n.p.	6 mya	n.p.(9+)	n.p.(6+)	n.p.(6+)	n.p.(6+)	6+mya	5+mya	(6+)	5mya	5mya	2+mya	4+mya	4mya

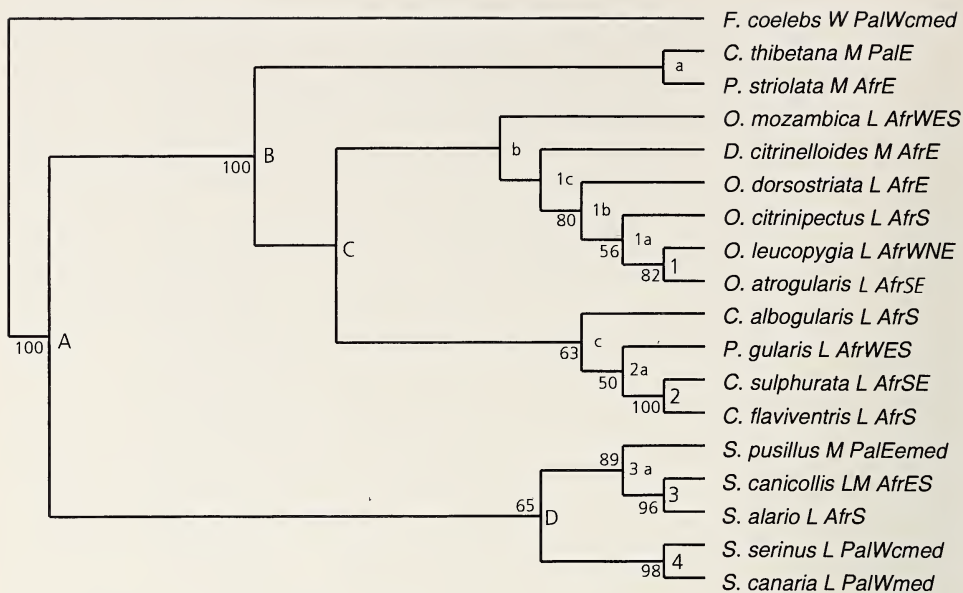


Fig.2: Neighbour-joining bootstrap tree from Arnaiz-Villena et al. (1999, fig.1b), slightly modified. Neighbour-joining (1000 replications) based on 924 bases of mtcyt b genes from 17 canary species and *Fringilla coelebs*. Bootstrap values above 50 are shown. For details see text.

tion of the areas of canary diversity coincides with endemic bird areas already outlined for Africa by Bibby et al. (1992) and Stattersfield et al. (1998) and with areas of primary montane and temperate floristic elements (Miehe & Miehe 1994, Wickens 1976). Ecological requirements in terms of food plant species were not discussed but may count as a limiting factor as most of the canary species are pure seedeaters and thus dependent on food plants, but the requirements of only a few species are as yet documented, including generalists (*Serinus syriacus*, Khoury 1998a,b) as well as specialists (*Poliospiza leucoptera*, Milewsky 1976, 1978). Provided with a new hypothesis of "*Serinus*" phylogeny, the neighbour-joining tree of Arnaiz-Villena et al. (1999) was chosen to test topographical and geographical distributions of canary lineages under the vicariance model again. The neighbour-joining tree was favoured because of its convincingly high bootstrap values. Moreover it depicts the phylogeny of genera suggested by the analysis of behavioural and morphological characters carried out by van den Elzen & Khoury (1999). It is presented in fig.2 with slight differences from the original: the two non-passerine species are omitted and nodes for nominate *Serinus c. canicollis* - *S. canicollis flavivertex* and of *Serinus canaria* for wild and domestic forms suppressed.

Under the premises of the vicariance model, nearest neighbours showing up in the dendrogram should verify the following characteristics: allopatric ranges, similarity in their topographic distribution and broad habitat requirements if they are young nodes. Deep nodes in contrast are allowed to display either sympatry, broad habitat differentiation, or lowland-montane divergence, or even show

differentiation in all premises within but not between subclusters. Results of an analysis of the molecular tree are summarized in table 2, and details are also shown in fig.2.

For the first-species pair supported by high bootstrap ancestral nodes, *Serinus canaria*-*S. serinus*, (fig.2: 4) ranges are allopatric with a small parapatric zone and their ecological requirements are roughly similar, with *S. serinus* having a larger range in more diverse habitat types and at lower elevations. In the *S. alario-canicollis*-*pusillus* clade (fig.2: node 3a) distribution patterns are puzzling. The allopatry argument is proven, two montane species combined with a lowland form, two Afrotropical canaries combined with a Palearctic species. *Serinus canicollis* and *alario* overlap in distribution in the southernmost parts of their range, where they even associate in mixed-species flocks.

If the distribution patterns of the entire *Serinus* clade (fig.2: node D) are investigated, no range overlap between the species can be found.

The second well-established pair by bootstrap is *Crithagra flaviventris-sulphurata* (fig.2: node 2). Species ranges are allo- to parapatric, overlap occurs in the southernmost part of range, but breeding habitats differ distinctly in the sympatric situation, *C. sulphurata* preferring in general moister habitats at higher altitudes than *C. flaviventris*. The assemblage of *C. sulphurata*-*flaviventris* plus *P. gularis* (fig.2: node 2a) together with *C. albogularis* (fig.2: node c) sketches a situation not as easily interpreted. *P. gularis* and *C. albogularis* both share the *flaviventris* habitat demands, and the ranges of the congeners *albogularis* and *flaviventris* overlap.

In the third high bootstrap node (*O. leucopygia*-*O. atrogularis*, fig.2: 1) species with allopatric distribution are again combined: both are savanna inhabitants, *O. leucopygia* living in the drier environment. The taxa adjoined to this species pair in node 1b and 1a by also high bootstrap, *O. citrinipectus* and *dorsostriata*, are allopatric and have roughly equal ecological requirements. If *mozambica* and *D. citrinelloides*, their nodes (fig.2: 1c, b) are of low significance, are joined, the latter, as a montane element, is allopatric to all other taxa and prefers woodland. *O. mozambica* – as the most widespread species – occurs in sympatry with *atrogularis*, *leucopygia* and *citrinipectus* (not with *dorsostriata*!), but is found in moister environments. As this species is allopatric to *dorsostriata*, Hall & Moreau (1970) placed both into one superspecies, the *atrogularis*-group comprising the species *atrogularis* (including *reichenowi* and *xanthopygia*), *leucopygia*, *citrinipectus*, as well as *flavigula* into a second one.

The last node (fig.2: a) supports faintly (since it is only of low significance, its bootstrap values are below 50 and are not given by Arnaiz-Villena et al. 1999) the relationship of *C. thibetana* and *P. striolata*. Both species are disjunct, occurring in high altitudes of different biogeographical regions.

Summarizing, it may be concluded that best results (i.e. high bootstrap values, tree stability, concordance with the vicariance model and systematics deduced from the morphological approach) are in the younger nodes, with the exception of node A. The suggested phylogenetic relationships of species in clusters with nodes of low bootstrap values, with inconsistent arrangements according to the algorithms used, are in most cases also contradicted by inconsistent distribution patterns and

broad habitat requirements of the species concerned. Deep nodes (B, C and partly a) are seemingly more difficult to prove than younger ones (from 6 Mya on).

Following the HENNIG 86 tree-topology of genera (van den Elzen & Khoury 1999), *Serinus* s.str. had to be the phylogenetically older clade. The ancestor of this taxon entered Africa south of the Sahara, where radiation of *Ochrospiza*, *Poliospiza*, *Dendrospiza* and *Crithagra* was favoured by mainly Pleistocene climatic changes, whereas *Serinus* s.str.-species (e.g. *Serinus canicollis*) entered the Afrotropics in a second immigration wave (see also van den Elzen 1985).

From their calculations of the phylogenetic age of different canary "lineages", Arnaiz-Villena et al. (1999) concluded that the "*Serinus*"-lineage s.lat. appeared in the Miocene and that Pleistocene glaciations may have driven subspeciation only, the majority of genera in the nomenclature of van den Elzen & Khoury (1999) being already present in their ancestral forms 6-7 Mya. These authors discuss an Asian origin for "*Serinus*", an old hypothesis favoured by Mayr (1946) and Marten & Johnson (1986) for other Carduelidae. Research on this topic will have to continue.

References

- Arnaiz-Villena, A., M. Alvarez-Tejedo, V. Ruiz-del-Valle, C. Garcia-de-la-Torre, P. Varela, M.J. Recio, S. Ferre & J. Martinez-Laso (1999): Rapid radiation of Canaries (Genus *Serinus*). – Mol. Biol. Evol. 16: 2-11.
- Ash, J.S. & J.E. Miskell (1998): Birds of Somalia. – Pica Press, Sussex.
- Bibby, C., N.J. Collar, M.J. Crosby, M.F. Heath, C. Imboden, T.H. Johnson, A.J. Long, A.J. Stattersfield & S.J. Thirgood (1992): Putting biodiversity on the map: priority areas for global conservation. – Cambridge, U. K. (International Council for Bird Preservation).
- Clement, P., A. Harris & J. Davis (1993): Finches and Sparrows, an identification guide. – Christopher Helm & Black, London
- Elzen, R. van den (1985): Systematics and evolution of African canaries and seedeaters (Aves: Carduelidae). – pp. 435- 451 in: Proc. Intern. Symp. African Vertebr. (ed. Schuchmann, K.-L.).- Bonn.
- Elzen, R. van den & F. Khoury (1999): Systematik, phylogenetische Analyse und Biogeographie der Großgattung *Serinus* Koch, 1816 (Aves, Carduelidae). – Cour. Forsch. Senck. 135: 55-65.
- Gatter, W. (1997): Birds of Liberia. – Pica Press, Sussex.
- Hall, B.P. & R.E. Moreau (1970): An atlas of speciation in African passerine birds. – British Museum of Natural History, London.
- Harrison, J.A., D.G. Allan, L.G. Underhill, M. Herremans, A.J. Tree, V. Parker & C.J. Brown (1997): The Atlas of Southern African Birds. – 2vols. BirdLife South Africa, Johannesburg.
- Irwin, M.P.S. (1964): An african canary superspecies. – Occas. Pap. Nat. Mus. S. Rhodesia 4 (27B): 16-25.
- Khoury, F. (1998a): Habitatwahl und Nahrungsökologie des Zederngirlitzes *Serinus syriacus* in Jordanien. – Dissertation, Bonn.

- Khoury, F. (1998b): Habitat selection by Syrian Serin *Serinus syriacus* in south-west Jordan. – Sandgrouse 20(2): 87-93.
- Lewis, A. & D. Pomeroy (1989): A Bird Atlas of Kenya. – A.A. Balkema, Rotterdam, Brookfield.
- Marten, J. & N. K. Johnson (1986): Genetic relationships of North American Cardueline finches. – Condor 88: 409-420.
- Mayr, E. (1942): Systematics and the Origin of Species. – Columbia University Press, New York.
- Mayr, E. (1946): History of North American bird fauna. – Wilson. Bull. 58: 4-41.
- Mayr, E. (1992): A local flora and the biological species concept. – Amer. J. Bot. 79: 222-238.
- Miehe, S. & G. Miehe (1994): Ericaceous forests and heathlands in the Bale Mountains of South Ethiopia, ecology and man's impact. – Traude Warnke Verlag, Hamburg.
- Milewsky, A. V. (1976): Feeding ecology and habitat of the Protea Seedeater. – MSc thesis, University of Cape Town, Cape Town.
- Milewsky, A. V. (1978): Diet of *Serinus* species in the southwestern Cape, with species reference to the Protea Seedeater. – Ostrich 49: 174-178.
- Mooers, A. O., R. D. M. Page, A. Purvis & P. H. Harvey (1995): Phylogenetic noise leads to unbalanced cladistic tree reconstruction. – Syst. Biol. 44: 332-342.
- Nelson, G. & G. Platnick (1981): Systematics and biogeography, cladistics and vicariance. – Columbia University Press, New York.
- O'Brien, E. M. (1998): Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. – J. Biogeogr. 25: 379-398.
- Paynter, R. A. (1968): Checklist of Birds of the World 14 (ed. J. L. Peters) . – Museum of Comparative Zoology, Cambridge U.S.A.
- Sibley, C. G. & B. L. Monroe (1990): Distribution and taxonomy of the birds of the world. – Yale University Press, New Haven U.S.A.
- Stattersfield, A. J., M. J. Crosby, A. J. Long & D. C. Wege (1998): Endemic Bird Areas of the world. – BirdLife International, Cambridge
- Wickens, G. E. (1976): The Flora of Jebel Marra (Sudan Republic) and its geographical affinities. – Kew Bull. Add. Ser. V: 1-368.
- Wolters, H. E. (1979): Die Vogelarten der Erde.- Paul Parey, Hamburg, Berlin.

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Patchy versus continuous distribution patterns in the African rain forest: the problem of the Anomaluridae (Mammalia: Rodentia)

Anja C. Schunke & Rainer Hutterer

Abstract: We investigated the distribution patterns of Anomalures (scaly-tailed squirrels), a family of gliding rodents confined to African old-growth forests. The evolution of these specialized mammals might be connected to the evolution of these forests. Current knowledge, however, does not allow conclusive confirmation of this assumption. Our analysis of both literature and specimen-based locality data has revealed two conflicting views of the distribution patterns of these animals. In most current textbooks the existence of broad continuous ranges throughout the African forest belt is postulated. By mapping actual locality data we found that patchy discontinuous distributions are equally supported. The contradictions are discussed for the respective countries in detail.

Key words: Anomaluridae, Rodentia, biogeography, African rain forest

Introduction

Anomalurids (or scaly-tailed squirrels) are highly specialized gliding rodents confined to African old-growth forests. Their existence depends on factors such as specific tree height, distance between trees and sufficient suitable tree holes. The evolution of these gliding mammals should thus be closely tied to the evolution of the African rain forest. Current knowledge, however, does not allow conclusive confirmation of this assumption.

Material and methods

For the analysis of the postulated distribution of Anomaluridae maps were taken from current textbooks (see below), enlarged to the same scale and the respective areas combined on a single map. The outlines in figs.1-3 give the maximum distribution assumed. Documented specimen-based localities were taken from various authors (see below), either redrawn from maps or from localities with given coordinates. Localities less than ca. 100 km apart were regarded as representing a continuous area and thus combined.

Distribution patterns

Our analysis of both literature and specimen-based locality data has revealed two conflicting views of the distribution patterns of these animals. In most current textbooks (McLaughlin 1984, Rahm 1988, Kingdon 1997) the existence of broad continuous distributions throughout the African forest belt is postulated (figs.1-3).

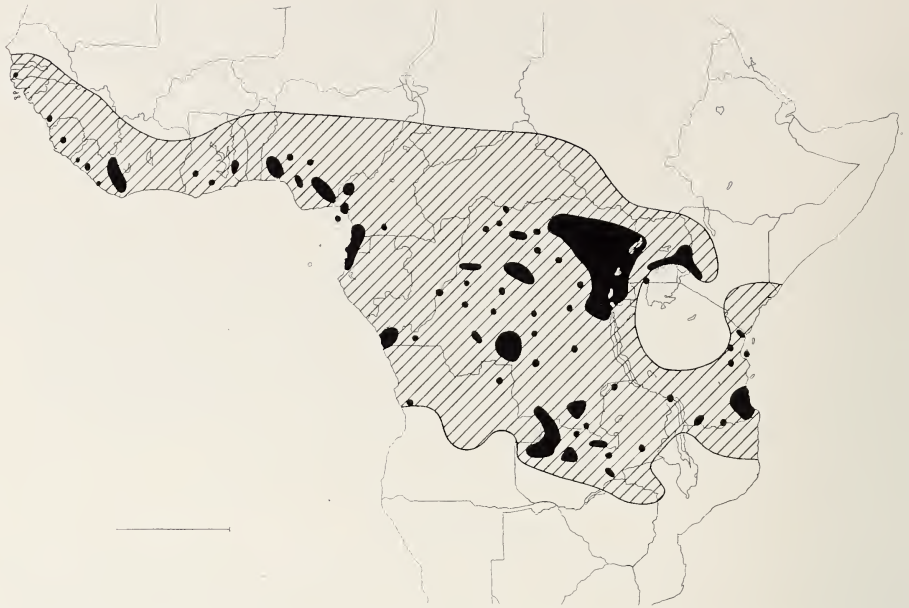


Fig.1: Presumed continuous distribution of the Anomalurinae as postulated by various authors (hatched area) contrasted with the documented localities (solid black areas); see text for references. Scale = 1000 km.



Fig.2: Presumed continuous distribution of *Idiurus* as postulated by various authors (hatched area) contrasted with the documented localities (solid black areas); see text for references. Scale = 1000 km.

By mapping actual locality data from the literature (Sanderson 1940, Rosevear 1953, Rahm 1960, Eisentraut 1963, Rahm & Christiaensen 1963, Verheyen 1963, Kuhn 1965, 1966, Rahm 1966, Rahm & Christiaensen 1966, Verheyen 1968, Jones 1971, Roche 1972, Kingdon 1974, Delany 1975, Ansell 1978, Happold 1987, Ansell & Dowsett 1988, Pérez del Val et al. 1995, Robbins & Van der Straeten 1996) and from voucher specimens we found that patchy discontinuous distributions are equally supported (figs.1-3). Our preliminary results thus suggest that the patterns of distribution in anomalurids are more complex. The discrepancy between assumed and real data differs among countries, therefore some areas will be discussed in detail in the following sections.

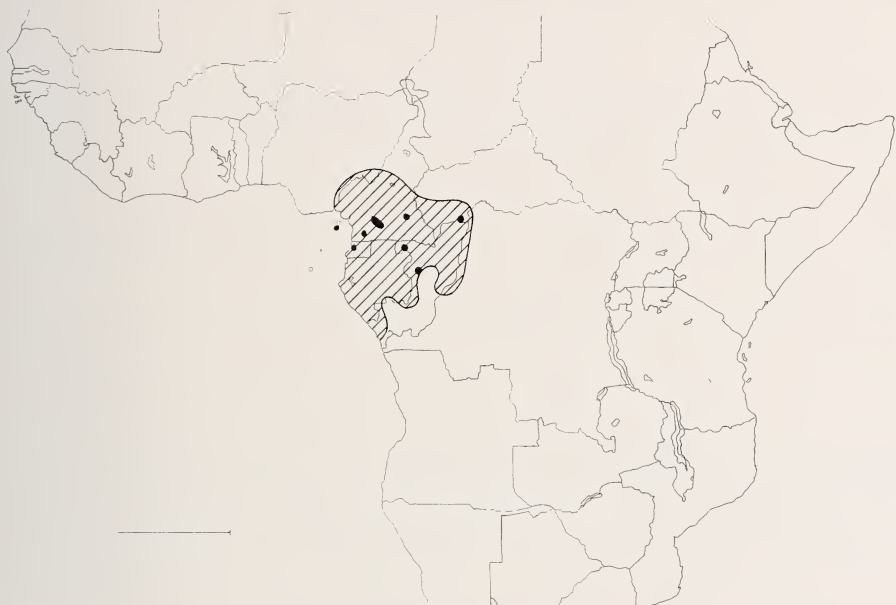


Fig.3: Presumed continuous distribution of *Zenkerella* as postulated by various authors (hatched area) contrasted with the documented localities (solid black areas); see text for references. Scale = 1000 km.

1. Senegal to Togo

In most current textbooks a broad belt of continuous distribution over West Africa is assumed, with a northwestern extension of Anomalurinae into The Gambia and Senegal, and an extension of *Idiurus* to Liberia. Contrary to the postulated distribution, documented localities from the western range of the Anomaluridae are extremely scattered. In most cases only a single animal was recorded, which often became the type specimen of a new taxon. Except for small clusters along the Liberia-Ivory Coast border and in Benin the specimen-based localities are usually isolated, with several hundred km distance between them. From The Gambia and Guinea-Bissau no findings are recorded.

Certainly the small number of records is partly due to the lack of expeditions to this area. But apart from this a broad continuous distribution is impossible because of the very scattered occurrence of rain forests. Particularly the postulated

distribution for *Idiurus* seems exaggerated, as it is only based on two isolated findings in Sierra Leone and Ghana.

2. Benin

Contrary to the postulated distribution of *Idiurus* and the Anomalurinae in this area no findings were recorded in the literature investigated. Analogous to the more western countries this may partly be due to the lack of collections, but in Benin the savanna extends down to the coastal region and separates the rain forest areas (Dahomey Gap: Grubb 1978, Robbins 1978), so in this country the occurrence of animals dependent on rain forest is unlikely.

3. Nigeria

This is the westernmost country with several observations of Anomalurinae, often less than one hundred km apart. Without a thorough investigation of additional material it is impossible to decide whether the gaps between the recordings are due to a lack of information or to the occurrence of an insurmountable obstacle. Despite numerous findings of Anomalurinae no *Idiurus* was recorded, which seems to indicate that the genus does not occur in this area, contrary to the postulated distribution.

4. Cameroon and Equatorial-Guinea

From these two countries findings of all groups of Anomaluridae are recorded. The distribution can be divided into several areas. Records of Anomalurinae and *Idiurus* originate from the Bambouto Mountains and the Cameroon Mountain in western Cameroon. The nearest findings to these are separated by a gap of some two hundred km and lie in southwestern Cameroon and western Equatorial Guinea and include Anomalurinae, *Idiurus* and *Zenkerella*. The island of Bioko is inhabited by at least two members of the Anomalurinae and *Zenkerella*, but no *Idiurus* is documented. From the center and east of southern Cameroon only a few scattered findings, mainly of *Zenkerella*, are recorded.

5. Gaboon, Congo and Central African Republic

In these countries the records are very rare and scattered, with findings of Anomalurinae near the northern coastal area of Gaboon and three widely separated localities for *Zenkerella*, two in Congo and one in the Central African Republic. Obviously the southern extent of the distribution of *Idiurus* and *Zenkerella* in Gaboon has been overestimated.

6. Democratic Republic of Congo and Cabinda

The records from this area are the most evenly distributed, at least for the Anomalurinae. From Cabinda and the extreme west of the Democratic Republic of Congo, between Popular Republic of Congo and Angola, several localities have been recorded, separated from the rest by a gap of some three hundred km.

The distribution of Anomalurinae in the main part of the Democratic Republic of Congo is difficult to interpret, because on the one hand the localities are very evenly distributed and on the other hand they show an average inter-locality distance of 100-150 km. As in the case of Nigeria, a better interpretation of the distribution pattern in the central Democratic Republic of Congo would require more information about these localities.

A different situation is found in the northeast of the country, where documented localities of Anomalurinae are usually less than 100 km apart. In this area a continuous distribution is very likely. The *Idiurus* records are more scattered, but an area that supports a continuous distribution of Anomalurinae may also provide suitable habitats for *Idiurus*. However a connection between the *Idiurus* population in the Congo Basin and that in West Africa, as postulated in the literature, is extremely unlikely. Although the region between the two areas was thoroughly investigated, no specimens were recorded; therefore the *Idiurus* population of the Congo Basin must be regarded as geographically separate from the population in Cameroon.

7. Angola

From Angola only two isolated findings are reported in the literature studied. Because it is mainly gallery forest that is available for anomalurids in this country, localities that do not belong to the same river system must be regarded as separated from one another.

8. Zambia

In western Zambia the situation is similar to Nigeria and central Congo: numerous records, some in clusters and obviously belonging to a continuous distribution, gaps of about 150 km between clusters, and also some isolated findings. No records are known from the southern part of Zambia, and only two isolated findings from the eastern part.

9. Rwanda and Burundi

From each of these countries a single finding is recorded. The locality in Rwanda is probably connected with the Anomalurinae distribution in Uganda, since the distance to the nearest locality there is just about 100 km.

10. Uganda and Kenya

The distribution in Uganda seems to be divided into two parts: the recorded localities near the border to the Democratic Republic of Congo very likely belong to the Anomalurinae area in northeastern Congo. Clearly separated from this area are the localities north of Lake Victoria in Uganda and Kenya.

11. Tanzania and Malawi

The Anomalurinae in Tanzania are separated from the populations of Kenya in the north and Zambia in the south respectively by gaps of more than 500 km, so a connection is very unlikely. Only one locality is known from Malawi.

Systematics

At present the 39 described taxa of the Anomaluridae are grouped into seven species (table 1). Our preliminary data, however, suggest that the taxon diversity has been underestimated. Some taxon names, such as the genus *Anomalurops* Matschie, 1914, will have to be resurrected.

Table 1: Concepts of the number of genera, species and subspecies of Anomaluridae from 1897 to 1997

Author	no of genera	no of species	no of subspecies
Trouessart 1897	2	10	–
Allen 1939	5	17	29
Ellerman 1940	4	9	25
Malbrant & Maclatchy 1949	5	8	10
Grassé & Dekeyser 1955	4	7	–
Rosevear 1969	4	7	15
Misonne 1971	3	7	–
Rahm 1988	3	7	20
Dieterlen 1993	3	7	–
Starck 1995	3	9	–
Kingdon 1997	3	7	–

Conclusions

The level of discrepancy between assumed and documented distributions differs between countries, but generally the presumed area appears to be an overestimate. Particularly the northern distribution of the Anomalurinae and the southern range of *Idiurus* and *Zenkerella* are not supported by recorded findings. In addition, well-known rain forest clearings such as the Dahomey Gap in Benin are often ignored. Sometimes all recorded localities of a taxon are presumed to belong to one continuous distribution area, even in cases where no findings were documented for some 1500 km, as in the genus *Idiurus*.

The analysis of distribution patterns in this group is also complicated by the lack of information due to the low level of zoological exploration of some areas, particularly in West Africa. For Nigeria, Cameroon and the Congo Basin countries, data from already existing museum specimens may solve some of the problems. Such data may support either separated clusters with clearly defined gaps or continuous distributions.

Another source of confusion regarding the distributions of the Anomaluridae is the controversial taxonomy of the group. It is sometimes impossible to tell which species (or even genus) an author refers to in a publication dealing with locality records.

Our further research will thus focus on the taxonomy and phylogeny of this interesting group of mammals in order to answer some of the questions encountered, particularly concerning their phylogeography.

References

- Allen, G. M. (1939): A checklist of African Mammals. – Bull. Mus. Comp. Zool. Harvard College 83: 1-763.
- Ansell, W. F. H. (1978): The Mammals of Zambia. – The National Parks & Wildlife Service, Chilanga, Zambia.
- Ansell, W. F. H. & R. J. Dowsett (1988): Mammals of Malawi. – The Trendrine Press, Zennor, U.K.
- Delany, M. J. (1975): The Rodents of Uganda. – Trustees of the British Museum (Natural History), London.
- Dieterlen, F. (1993): Family Anomaluridae. – pp. 757-758 in: Mammal Species of the World. A taxonomic and geographic reference. 2nd edition (eds. Don E. Wilson & DeeAnn M. Reeder). Smithsonian Institution Press, Washington, London.
- Eisentraut, M. (1963): Die Wirbeltiere des Kamerungebirges unter besonderer Berücksichtigung des Faunenwechsels in den verschiedenen Höhenstufen. – Paul Parey, Hamburg & Berlin.
- Ellerman, J. R. (1940): The families and genera of living rodents. Volume I: Rodents other than Muridae. – British Museum (Natural History), London.
- Grassé, P. P. & P. L. Dekeyser (1955): Ordre des Rongeurs. – pp. 1321-1525 in: Traité de Zoologie. Anatomie, Systematique, Biologie. (ed. Pierre P. Grassé). 17, 2, Paris.
- Grubb, P. (1978): Patterns of speciation in African mammals. – Bull. Carneg. Mus. nat. Hist. 6: 152-167.
- Happold, D. C. D. (1987): The mammals of Nigeria. – Clarendon Press, Oxford.
- Jones, C. (1971): Notes on the anomalurids of Rio Muni and adjacent areas. – J. Mammal. 52: 568-572.
- Kingdon, J. (1974): East African mammals. An Atlas of Evolution in Africa. Volume II Part B (Hares and Rodents). – Academic Press, London, New York.
- Kingdon, J. (1997): The Kingdon Field Guide to African Mammals. – Academic Press, London.
- Kuhn, H.-J. (1965): A provisional check-list of the mammals of Liberia. – Senckenbergiana biol. 46: 321-340.
- Kuhn, H.-J. (1966): *Anomalurus pelii auzembergeri* in Liberia. – J. Mammal. 47: 334-338.
- Malbrant, R. & A. Maclatchy (1949): Faune de l'Équateur Africain Français. Tome 2. Mammifères. Encyclopédie biologique 36. Lechevalier, Paris.
- McLaughlin, C. A. (1984): Protogomorph, Sciurormorph, Castorimorph, Myomorph (Geomyid, Anomalurid, Pedetoid, and Ctenodactyloid) Rodents. – pp. 267-288 in: Orders and families of recent mammals of the world (eds. S. Anderson & J. Knox Jones Jr.). John Wiley & Sons, New York: 267-288.
- Misonne, X. (1971): Rodentia. – pp. 1-39 in: The Mammals of Africa. An identification Manual (eds. J. Meester & H. W. Setzer). Smithsonian Institution Press, City of Washington.

- Pérez del Val, J., J. Juste & J. Castroviejo (1995): A review of *Zenkerella insignis* Matschie, 1898 (Rodentia, Anomaluridae). First records in Bioko island (Equatorial Guinea). – *Mammalia* 59: 441-443.
- Rahm, U. (1960): L' *Anomalurus jacksoni* de Winton: Répartition, biologie et observations en captivité. – *Bull. Soc. Roy. Zool. Anvers* 18: 3-13.
- Rahm, U. (1966): Les mammifères de la forêt équatoriale de l'Est du Congo. – *Ann. Mus. Roy. Afr. Centr.* 149: 39-121.
- Rahm, U. (1988): Dornschwanzhörnchenverwandte. – pp. 116-125 in: Grzimeks Enzyklopädie Säugetiere (ed. B. Grzimek). Kindler Verlag, München, Band 3.
- Rahm, U. & A. Christiaensen (1963): Les mammifères de la région occidentale du lac Kivu. – *Ann. Mus. Roy. Afr. Centr.* 118: 1-83.
- Rahm, U. & A. Christiaensen (1966): Les mammifères de l'île Idjwi (Lac Kivu, Congo). – *Ann. Mus. Roy. Afr. Centr.* 149: 1-35.
- Robbins, C. B. (1978): The Dahomey Gap – a reevaluation of its significance as a faunal barrier to West African high forest mammals. – *Bull. Carneg. Mus. nat. Hist.* 6: 168-174.
- Robbins, C. B. & E. Van der Straeten (1996): Small mammals of Togo and Benin. – *Mammalia* 60: 231-242.
- Roche, J. (1972): Capture de *Zenkerella insignis* (Rongeurs, Anomaluridés) en République Centrafricaine. – *Mammalia* 36: 305-306.
- Rosevear, D. R. (1953): Checklist and Atlas of Nigerian Mammals with a foreword on Vegetation. – F. Howard Doulton & Co., London.
- Rosevear, D. R. (1969): The rodents of West Africa. – British Museum (Natural History), London.
- Sanderson, I. T. (1940): The mammals of the North Cameroons forest area. – *Trans. Zool. Soc. Lond.* 24: 623-725.
- Starck, D. (1995): Lehrbuch der speziellen Zoologie. Band 2, Teil 5/2: Säugetiere. – Gustav Fischer Verlag Jena.
- Trouessart, E.-L. (1897): Catalogus Mammalium tam viventium quam fossilium. Fasciculus I. – Berolini, R. Friedländer & Sohn.
- Verheyen, W. N. (1963): Contribution à la systématique du genre *Idiurus* (Rodentia-Anomaluridae). – *Rev. Zool. Bot. Afr.* 68: 157-197.
- Verheyen, W. N. (1968): The Anomalurinae of the Congo (Rodentia: Anomaluridae). – *Rev. Zool. Bot. Afr.* 77: 392-411.

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Non-insect Arthropoda (Isopoda, Arachnida and Myriapoda) on the high mountains of tropical Africa

Petar Beron

Abstract: For the first time an overview is given of the distribution of non-insect arthropods (Isopoda, Arachnida and Myriapoda, or IAM) of the montane zone of tropical Africa: Mt Cameroon, Mt Kenya, Kilimanjaro, Ruwenzori, Mt Elgon, Mt Meru and some Ethiopian mountains including Semien. Although "montane" is usually defined as the area above the forest, here we arbitrarily indicate two lines above which the fauna is analyzed: 2200 m (allowing comparison with the Eurasian oréal) and 3500 m, above which throughout the world lower atmospheric pressure, higher UV radiation and the same ecological factors are present. We present the montane fauna of Isopoda, Arachnida and Myriapoda of the Afrotropical oréal and compare it with the fauna of those zones in the northern regions of the Old World, e.g. Europe, Himalaya and Central Asia.

We list in the appendix all species of IAM found in Africa above 3500 m and thus give a complete list of all hypsobionts so far described.

In Africa, we found IAM up to 4600 m (Isopoda), 2600 m (Schizomida), 3500 m (Scorpionida), 4100 m (Pseudoscorpionida), 4600 m (Opilionida), 4930 m (Araneida), 4590 m (Acari), 4500 m (Symphyla), 4500 m (Chilopoda), and 4200 m (Diplopoda). The level of endemism is low and, at least concerning the IAM, the Afrotropical montane fauna does not form a separate zoogeographical unit. Comparisons between the IAM of the Afrotropical oréal and the oreals of Europe, Central Asia and the Himalaya present a very diversified pattern. This phenomenon is discussed under evolutionary aspects.

Key words: Afrotropical oréal, Isopoda, Arachnida, Diplopoda, Chilopoda, Symphyla, biodiversity

Introduction

While there are several important studies on the ecology of the insect life at high altitude (especially by Mani 1968, centred on the Himalayan fauna), no attempt is known concerning such important groups as the non-insect arthropods (essentially Isopoda: Oniscidea, Arachnida and Myriapoda). Most of the recent contributions to these groups are based on the rich collections of J. Martens and other zoologists from the Himalaya. But the high mountains of Africa have also been investigated by many expeditions and we can now put together the available information and try to come to some conclusions.

For several decades the author has explored high mountains in all continents and so has had the chance to get a personal impression of the high mountain environment, as well as to collect important series of Isopoda, Arachnida and Myriapoda, most of which are still under study. This research also included tropical West, Central and East Africa (the mountains of Cameroon, the Ruwenzori, Kilimanjaro and Mt Elgon).

Here under “high mountains of East and Central Africa” we understand the mountains north of the Zambezi, east of 30°E and south of Egypt. In this area the highest mountains in Africa are situated: the volcanos Kilimanjaro (5895 m), Mt Kenya (5199 m), Mt Meru (4567 m), Karisimbi (4507 m), Mt Elgon (4322 m), and the massif of Ruwenzori (5109 m). Some other high mountains in this area are: in Tanzania: Uluguru (2653 m), Ngorongoro (Lulmalasin 3648 m, Oldeani 3188 m), Usumbura (2570 m), Pare (2463 m), Kipengere (Mtorwi 2961 m), and Rukwa (Tapepo 2694 m); in Kenya: Aberdare (Satima 3963 m, Kinangop 3960 m); and in Malawi: Sapitva (3000 m). Aberdare is only 100 km distant from Nairobi and is therefore well explored. Mt Elgon has also been visited by collectors of ground fauna. Larger collections of IAM exist only from Kilimanjaro, Mt Kenya, Mt Meru, Mt Elgon, Ruwenzori, and Aberdare (see fig.1).

The mountains of Ethiopia are much less explored, but are very interesting from a zoological point of view. The highest tops are situated in the Semien massif (Ras Dashan 4623 m), followed by Mandebo (4310 m in the Bale National Park), Guna (4231 m), Guge (4203 m), Kakka (4193 m), Abune Josef (4193 m), and Mangestu (Tala 4100 m). The Semien mountains were glaciated up to 2600 m. Fako (height 4090 m) is the highest summit of the volcano range on the border between West and Central Africa.

The zone with forest or higher scrub vegetation in the mountains ascends according to temperature and precipitation. At an altitude of 2200 m a.s.l. on every mountain in tropical Africa we find forest or a man-made landscape. But everywhere at 3500 m a.s.l. we find the conditions typical of the montane environment: lower atmospheric pressure, higher UV radiation and a vegetation adapted to these conditions. We present here the Isopoda, Arachnida and Myriapoda¹ fauna reaching or surpassing 2200 m to have the basis for a comparison with similar montane regions of the Old World. And we present the IAM fauna for 3500 m, the zone where the fauna consists of true hypsobionts.

In the following paragraphs we will give some general information on the distribution of IAM in the Old World (Africa plus Eurasia), with special reference to the montane regions of Europe, the Himalaya and Central Asia. Data on IAM in Africa are given here only if this is essential for the general overview. But every zoologist who is not specialized in IAM will have problems understanding the system of these non-insect athropods; this is especially true because the endings of classes, orders or suborders are often not self-explanatory (s. table 1).

Isopoda. In contrast to the high diversity of montane woodlice in Africa, the number of families, genera and species in the oreals of the rest of the Old World is rather poor. In the oreals of Europe and Asia there are no endemic families. The number of genera is much smaller and none is endemic. Out of 23 species known in the Old World occurring higher than 3500 m, 12 live in East and Central Africa.

¹) Myriapoda is used here as a superclass, including the classes Symphyla, Pauropoda, Chilopoda and Diplopoda; we know that Myriapoda possibly is not a real taxon, but a polyphylum.



Fig. 1: Map of Central and South Africa, showing the main elevations.

Arachnida. All 8 orders of Arachnida are known from the high mountains of the Old World and most from high altitudes in Africa (except Solpugida). They are also present in the orol of the Americas. The orders not represented in the montane fauna of Eurasia and Africa (Palpigradi, Amblypygi, Uropygi, Ricinulei, Opilioacarida), are also absent from the high mountains of the western hemisphere, although these orders do occur there at lower altitudes.

Table 1: The higher taxa of Isopoda, Arachnida and Myriapoda dealt with in this paper (the groups found in tropical Africa above 2200 m are in bold):

Class Crustacea	Superclass Myriapoda
Order Isopoda	Class Symphyla
Suborder Oniscidea	Class Pauropoda
Class Arachnida	Class Chilopoda
Order Schizomida	Order Lithobiomorpha
Order Scorpionida	Order Geophilomorpha
Order Solpugida	Order Scolopendromorpha
Order Araneida	Order Scutigleromorpha
Order Pseudoscorpionida	Class Diplopoda
Order Opilionida	Order Polyxenida
Suborder Laniatores	Order Glomerida
Suborder Palpatores	Order Craspedosomatida
Order Acariformes	Order Julida
Suborder Acaridida	Order Chordeumatida
Suborder Prostigmata	Order Stemmiulida
Suborder Oribatida	Order Spirostreptida
Order Parasitiformes	Order Polydesmida
Suborder Gamasida	
Suborder Ixodida	

Scorpionida. Five families in the Old World are known to contain species living over 2200 m. Some genera of Buthidae (*Uroplectes*, *Lychas*) are known to live up to 3500 m on Mt Meru and at 3000 m on Kilimanjaro. In South America, scorpions live much higher (*Orobothriurus crassimanus* Maury, family Bothriuridae, up to 5560 m in Peru). Polis (1990) writes: "Such high-elevation species are all small. They feed on a diverse array of arthropods that are also found at these heights (Mani 1968), and their small size may be due to the short period during which they are able to forage... 'Cold hardiness' allows at least some species to survive freezing temperatures. Surprisingly, high-altitude scorpions live under rocks, in scrapes, and in relatively short burrows (...), rather than in deep burrows with terminal chambers below the frost line".

Solpugida. At least five of the Old World families contain species living higher than 2200 m. In South America, other families of this order (Ammotrechidae) can reach even 5000 m (*Dasycleobis crinitus* Mello-Leitao in Argentina). The highest record for the Old World is of *Galeodes setulosus* Birula from Tajikistan (4000 m).

Schizomida. These small arachnids are warm-loving and clearly avoid the high mountain environment. The highest record (2600 m) is from Tanzania (Reddell & Cokendolpher 1995).

Pseudoscorpionida. This order shows a high diversity all over the montane regions of the Old World. However table 2 demonstrates that the different families and genera have their typical distribution; none is evenly spread over the four regions.

Table 2: Number of species of different genera and families of Pseudoscorpionida living at or above 2200 m in Europe, Central Asia, Himalaya and tropical Africa

	Europe	Centr. Asia	Himalaya	Africa		Europe	Centr. Asia	Himalaya	Africa
Chthoniidae	3	1	2	2	Cheiridiidae	0	0	2	3
<i>Centrochthonius</i>	0	1	0	0	<i>Apocheiridium</i>	0	0	1	1
<i>Chthonius</i>	3	0	0	0	<i>Cheiridium</i>	0	0	1	0
<i>Lagynochthonius</i>	0	0	1	0	<i>Cryptocheiridium</i>	0	0	0	2
<i>Tyrannochthonius</i>	0	0	1	2					
Lechytiidae	0	0	1	1	Atemnidae	0	1	2	9
<i>Lechytia</i>	0	0	1	1	<i>Atemnus</i>	0	1	2	0
					<i>Cyclatemnus</i>	0	0	0	4
Tridenchthoniidae	0	0	1	3	<i>Micratemnus</i>	0	0	0	1
<i>Compsaditha</i>	0	0	0	1	<i>Paratemnoides</i>	0	0	0	1
<i>Ditha</i>	0	0	1	0	<i>Titanatemnus</i>	0	0	0	3
<i>Pycnodithella</i>	0	0	0	1					
<i>Verrucadithella</i>	0	0	0	1	Cheliferidae	0	6	3	4
Geogarypidae	0	2	2	2	<i>Dactylochelifer</i>	0	5	1	0
<i>Afrogarypus</i>	0	0	0	2	<i>Gobichelifer</i>	0	1	0	0
<i>Geogarypus</i>	0	2	2	0	<i>Chelifer</i>	0	0	0	1
					<i>Hansenius</i>	0	0	0	1
Olpiidae	0	2	1	1	<i>Hysterochelifer</i>	0	0	1	0
<i>Calocheiridius</i>	0	0	1	1	<i>Lophochernes</i>	0	0	1	0
<i>Garypinus</i>	0	1	0	0	<i>Microchelifer</i>	0	0	0	2
<i>Olpium</i>	0	1	0	0					
Hyidae	0	0	5	0	Chernetidae	1	4	9	14
<i>Stenohya</i>	0	0	4	0	<i>Alochernes</i>	1	1	0	0
syn. <i>Laevigatocreagris</i>	0	0	1	0	<i>Caffrowithius</i>	0	0	0	5
					<i>Ceriochernes</i>	0	0	3	0
Neobisiidae	17	2	2	2	<i>Lasiochernes</i>	0	0	0	1
<i>Bisetocreagris</i>	0	2	1	0	<i>Dendrochernes</i>	0	1	1	0
<i>Microbisium</i>	0	0	0	1	<i>Lamprochernes</i>	0	0	1	0
<i>Neobisium</i>	16	0	0	1	<i>Megachernes</i>	0	1	3	0
<i>Nepalobisium</i>	0	0	1	0	<i>Nudochernes</i>	0	0	0	8
<i>Roncus</i>	1	0	0	0	<i>Orochernes</i>	0	0	1	0
					<i>Pselaphochernes</i>	0	1	0	0
Syarinidae	0	0	0	1					
<i>Ideoblothrus</i>	0	0	0	1	Withiidae	0	0	1	7
					<i>Ectromachernes</i>	0	0	0	1
					<i>Stenowithius</i>	0	0	0	1
					<i>Trichotowithius</i>	0	0	0	2
					<i>Withius</i>	0	0	1	3

Opilionida. The short-footed Cyphophthalmi do not live above 2000 m. The numerous species and genera belonging to Laniatores are confined mostly to tropical countries, including high mountains. In the mountains of tropical Africa, Laniatores are clearly predominant. In the high mountains of Europe, Laniatores do not live higher than 2000 m.

In the Old World 227 species of harvestmen (84 Laniatores and 143 Palpatores) reach or go higher than 2200 m. Here 11 families are known to exist, but much less

are true high mountain-dwellers and only three families of Laniatores contain true members of high mountain species: Phalangodidae, Biantidae and Assamiidae. The latter two families live also above 4000 m (Biantidae up to 4250 m in Nepal, Assamiidae up to 4600 m on Kilimanjaro). Between 2200 and 4000 m the number of genera and species almost halves every 500 m. Above 4500 m only one species was found: *Hypoxestus accentuatus* Sørensen (Assamiidae) on Kilimanjaro.

Table 3: The nine families of Old World Araneida living above 3500 m (listed according to altitude):

Lycosidae: 70 species up to 6100 m	Dictynidae: 9 species up to 4930 m
Salticidae: 85 species up to 5947 m	Thomisidae: 48 species up to 4880 m
Linyphiidae: 447 species up to 5545 m	Theridiidae: 24 species up to 4600 m
Hahniidae: 14 species up to 5181 m	Araneidae: 23 species up to 4500 m
Gnaphosidae: 74 species up to 4980 m	

Araneida. High-altitude spiders belong almost exclusively to the suborder Araneo-morphae. The only three species (all African) of the suborder Mygalomorphae are not known from localities higher than 2500 m. Above 3500 m only representatives of Araneomorphae are met. The nine families, reaching or surpassing 4500 m, outline the habitus of the spider fauna in the highest regions of the Old World. They contain 794 of the total of 904 species of spiders living above 2200 m in the Old World (table 3).

Table 4: Number and percentage of species of the family Linyphiidae that reach or surpass different altitudes of the total of Araneida species

altitude	Araneida	Linyphiidae	
	no. of species	no. of genera	no. of species (percentage)
2000 m a.s.l.	904		447 (49,6%)
3000 m a.s.l.	351	57	179 (51%)
4000 m a.s.l.	74	18	37 (50%)
5000 m a.s.l.	10	3	3 (33%)

From these data we can see that the bulk of species living in all high mountains of the Old World belong to the family Linyphiidae (s.lat.).

Clearly none of the genera can be considered to be dominant in the high mountains of the Old World, except *Lepthyphantes* s.lat., which contains 10 % of all high altitude spiders and was recorded up to 5545 m. *Pardosa* and *Xysticus* also have many species widespread in higher altitudes.

Acariformes. All three suborders occur in high mountains. The present maximum recorded altitude is 6100 m (in Nepal). – Acaridida are not well studied.

Prostigmata are represented at altitudes above 2200 m in the Old World by not less than 256 species in 95 genera and 31 families (a tiny fraction of the

prostigmatic mites known in the world with more than 14 000 species in 140 families and 1100 genera). The most species-rich are the families of Trombiculidae (53), Trombidiidae (41), Erythraeidae (38), Bdellidae (18) and Rhagidiidae (18). The genus *Balaustium* (Erythraeidae) contains the most species (19). The families of the Prostigmata are cosmopolitan. Seventeen of them reach 3000 m, 11 (with 23 genera and 35 species) 3500 m, seven 4000 m, four 4500 m, and one 5000 m. None of all identified prostigmatic mites was recorded up to 6100 m. The highest records are of Adamystidae (5100 m in the Hindu Kush), Anystidae (4950 m in Nepal), Rhagidiidae (4800 m on Kilimanjaro), Pygmephoridae (4500 m in New Guinea), Erythraeidae (4260 m in New Guinea), Trombidiidae (4200 m on Ruwenzori), Trombiculidae (4155 m in Pakistan). With more intense research the upper limit of Bdellidae and other families most probably will rise. The bulk of the material so far collected remains unidentified due to the lack of specialists.

Oribatida. Among the montane Acariformes, the soil-inhabiting species of the suborder Oribatida are most numerous. With their 66 families found at or above 2200 m, the Oribatids are the most diversified suborder of all high-altitude Arthropods, even more varied than the spiders. In the whole world more than 7000 oribatid mites have been described, belonging to 177 families. Their importance in natural ecosystems is enormous (in some places more than 70 % of all soil mites). Together with the theoretical interest they represent, this has led to an intensive research of the group by many specialists. The families Oppiidae (36), Ceratozetidae (33), and Phthiracaridae (18) contain most species. With increasing altitude the number of families and species decreases (table 5).

Table 5: Decrease of Oribatida (families and species in the Old World) with increasing altitude

> 2200 m: 66 families, 328 species	> 4500 m: 16 families, 19 species
> 3000 m: 41 families, 116 species	> 5000 m: 13 families, 15 species
> 3500 m: 31 families, 70 species	> 5500 m: 9 families, 11 species
> 4000 m: 19 families, 28 species	

Oribatida have been recorded in the Himalaya as high as 6100 m (Janetschek 1990). This author found in Nepal at up to 5800 m representatives of the families Brachychthoniidae, Hermannidae, Damaeidae, Ceratoppiidae, Tectocephidae, Suctobelbidae, Oribatulidae, Ceratozetidae and at up to 5500 m Oribatellidae, which are not yet identified to species level. Certainly at 5000 m tens of species live which are at the base of the scarce nival biota.

Parasitiformes. All three suborders in this order are known from high mountains of the Old World. The Gamasida form the bulk of representatives of the order Parasitiformes, but they are as yet poorly studied, except the fauna of the Alps. Several species (mostly parasites and commensals on mammals) have been recorded from only a few places (Hindu Kush up to 4550 m, Kilimanjaro up to 4285 m). Members of at least eight families live higher than 3000 m: Parasitidae, Macrochelidae, Halolaelapidae, Zerconidae, Rhodacaridae, Hypoaspidae, Dermanyssidae, Laelapidae. Two of the three families of the suborder Ixodida are known from the montane environment (parasites on birds and mammals). Thanks to intensive research of the Himalayan fauna between 1960 and 1980 mainly by H.

Hoogstraal and his colleagues, Argasidae have been found up to 4575 m in Nepal and Ixodidae as high as 5488 m. *Ixodes berlesei* (on the Snow Partridge *Lerwa lerwa* in Nepal at 5488 m) is the highest representative of the Parasitiformes ever found.

Symphyla. With about 160 species this is a small class. Both of its families (Scolopendrellidae and Scutigerellidae) live in all high mountain regions of the world and are represented in this environment with a total of 25 species. The genus *Hanseniella* prevails in the tropical mountains and is practically the only genus of Symphyla known to live in the mountains above 3000 m.

Chilopoda. The centipedes contain about 2800 known species of which at least 80 live in the Old World above 2200 m.

Identified species of Geophilomorpha in the Old World are known up to 3600 m (*Tygarrip nepalensis* Shinohara, Mecistocephalidae, Nepal), but Janetschek (1990) has collected Geophilidae in Nepal even at 4400 m. Our observations confirm the occurrence of Geophilomorpha at high altitudes. The genus *Schendylurus* has been recorded in Peru slightly higher (4500 m).

Scolopendromorpha reach 4000 m on Mt Elgon (*Scolopendra afra* Mein.), 4500 m in Nepal (*Cryptops doriae* Pocock) and 4150 m in the Andes.

The representatives of Lithobiomorpha (Lithobiidae) reach the highest altitude of all Myriapoda (up to 5700 m in the Himalaya). They are the most numerous within the four classes of Myriapoda and one of the most conspicuous arthropods in the high mountains of Eurasia. Only one other family of Lithobiomorpha has been recorded from considerable altitudes – two species of the genus *Lamycetes* (Henicopidae) reach 4000 m, one occurs above 4000 m in the mountains of tropical Africa.

Scutigeromorpha reach 4250 m in Nepal (our unidentified collections); they are not recorded from high altitudes in Africa.

Diplopoda. Out of the total of 16 orders in the class Diplopoda, 12 include species that are found above 2200 m in the Old World. As far as we know, in the orders Glomeridesmida, Platydesmida, Spirobolida and Siphoniulida no species are found at that altitude. Out of more than 12 000 species of Diplopoda described in the world, at least 237 have been recorded in the Old World from altitudes higher than 2200 m, including 20 from the mountains of tropical Africa.

Material and method

We summarized the available information from the literature on the species of Isopoda, Arachnida and Myriapoda in Africa living higher than 2200 m. This dataset was completed by data obtained by our own collecting in the mountains of tropical Africa:

- in December 1977 from Buea to the top of Fako, the summit (4090 m) of Mount Cameroon, and on the island of Bioko (formerly Fernando Poo) on the slopes of Pic de Malabo (3008 m)
- in 1983 on Kilimanjaro in Tanzania
- in 1993 on Ruwenzori in Uganda and Mt Elgon in Kenya.

We also collected on many European mountains, in the Karakorum, Himalaya and other mountains in Asia. Here, too, the available information in the literature was gathered. When comparing of the oreals of Africa, Europe, Himalaya and Central Asia, special attention was paid to the distribution of IAM in different altitudinal belts. Parts of the collected material is still under study and therefore does not appear in the lists and in the different comparisons.

Within the accounts there is some help for the reader: classes and orders, when they are named for the first time, are in bold and suborders are underlined.

Isopoda, Arachnida and Myriapoda in the mountains of tropical Central and East Africa

When we here describe the IAM from the montane Afrotropis so far identified, some aspects should be kept in mind: a great number of species, genera, families, or orders are known from lowland Africa. In most cases we do not point out that the taxon may occur elsewhere in Africa but that it is absent from the tropical mountains. The conclusions about endemism would change considerably if we were to include lowland taxa.

Isopoda

The essential information on the woodlice of the mountains of East Africa comes from the collections of the Swedish Expedition of Y. Sjöstedt in 1905-1906 (identified by Budde-Lund), from the material collected by R. Jeannel and the other participants to the Omo Expedition (identified by L. Paulian de Félice), from the collection of H. Franz (published by K. Schmölzer), and from the results of the Zoological Mission in East Africa of IRSAK (P. Basilewsky and N. Leleup), the material having studied by F. Ferrara and S. Taiti. Data on the terrestrial Isopoda of the high mountains of Ethiopia can be found in the paper by Barnard (1940), who identified the material collected by J. Omer-Cooper in 1926-27, as well as in the interesting note by A. Vandel in the general paper by Scott (1958). The species of the well-explored East and Central African mountains (Ruwendzori, Mt Elgon, Mt Kenya, Kilimanjaro, Aberdare, Uluguru, etc.) are well known, whereas we have little information about Ethiopia and Malawi, and the fauna of Mt Cameroon above 3000 m is still unexplored. Considerable material, presently being identified in Florence, was also collected by us on the mountains of Kilimanjaro, Mt Elgon and Ruwendzori.

At the moment we know that 66 species of Isopoda in Afrotropical mountains reach or surpass 2200 m: Mt Elgon 9 species, Kilimanjaro 12, Mt Meru 11, Ruwendzori 3, Nyiragongo 2, Aberdare 6, Kivu 1, Uluguru 7, Mt Kenya 4, Ethiopia 4, Malawi 6, Mt Fako 1. At least 42 species live above 2500 m, 23 above 3000 m, 11 above 3500 m and 5 at or above 4000 m.

In the East and Central African mountains above 2200 m there are at least 49 species belonging to 27 genera and five families. These are: Philosciidae (*Afrophiloscia*, *Uluguroscia*, *Arcangeloscia*, *Pleopodoscia*, *Buddelundiscus*), Porcellionidae (*Thermocellio*, *Uramba*, "*Porcellio*"), Oniscidae (*Alloniscus*), Eubelidae (*Eubelum*, *Gelsana*, *Gerutha*, *Rufuta*, *Periscyphops*, *Stegosauroniscus*, *Benechinus*, *Kenyoniscus*, *Periscyphis*, *Mesarmadillo*, *Hiallum*, *Hiallelgon*,

Arthiopopactes, *Oropactes*, *Microcercus*) and Armadillidae (*Pseudodiploexochus*, *Ctenorillo*, “*Synarmadillo*”). Twelve genera in four families (Eubelidae 9, Philosciidae 1, Porcellionidae 1, and Armadillidae 1) reach or surpass 3500 m.

The tropical family Eubelidae contains the highest number of genera and species living in high mountains. Eighteen genera contain species that live above 2200 m. The highest living are *Aethiopopactes* Verh (*Ae. chenzemae*) (4600 m on Kilimanjaro) and *Benechinus* Budde-Lund (*B. armatus*) (4600 m on Mt Meru), but also in the genera *Eubelum*, *Hiallelgon*, *Hiallum*, *Mesarmadillo*, *Periscyphis*, and *Microcercus* there are species recorded from altitudes at or over 3500 m.

Genera of Isopoda endemic to the Afrotropical mountains are *Benechinus*, *Gerutha*, *Hiallelgon*, *Hiallum*, *Kenyoniscus*, *Stegosauroniscus*, (Eubelidae), and *Ctenorillo* (Armadillidae). High altitude endemics are *Benechinus* (only on Meru and Kilimandjaro, 2200-4600 m), *Stegosauroniscus* (Meru, 2200-2600 m, Kilimandjaro, 2200 m) and others.

All 66 Isopoda species from Afrotropical mountains above 2200 m are endemics. Most species obviously occur only on one massif. Species that were collected from two mountain massifs are: *Afrophiloscia uncinata*, *Stegosauroniscus horridus*, *Benechinus armatus* (Kilimanjaro and Meru, which are close together but nevertheless separated by savanna) and *Oropactes maculatus* (Uluguru and mountains in Malawi).

Arachnida

Scorpionida. Some genera of the family Buthidae (*Uroplectes*, *Lychas*) are known to live at up to 3500 m on Mt Meru and at 3000 m on Kilimanjaro.

Solpugida. Although this order is well represented in Africa, none of its many species is known to live in this continent higher than 2200 m (lack of research?).

Schizomida. These small Arachnids are warm-loving and clearly avoid the high mountain environment. They have been found at up to 2600 m in Tanzania (Reddell & Cokendolpher 1995). Since at this altitude we find the usual vegetation cover we think that Schizomida are not a part of the hypsobionts of Africa.

Pseudoscorpionida. The studies of Tullgren, Beier, Mahnert, Redikorzev and our own collecting in Kenya, Tanzania and Uganda have shown that 56 species (in 25 genera and 13 families) live at or above 2200 m in East and Central African mountains; 22 reach 3000 m, six 3500 m and one is known to live above 4000 m.

Of the 56 species above 2200 m, almost all are endemic to the mountains of the Afrotropis (see footnote p. 166), but there are almost no endemic genera: *Trichotowithius* (Withiidae) is known only from two high-mountain species (above 2100 m), one in Ethiopia another on Mt Elgon. Most of the remaining genera are widespread in Africa, some of them even outside the continent.

Besides the two species of *Trichotowithius*, we can consider as hypsobionts four species of the genus *Nudochernes* (*N. nidicola* 2470-3000 m, *N. montanus* 3500 m, *N. crassus* 3000-3700 m, and *N. granulosus* 2600 m) inhabiting the nests of *Tachyoryctes* (Rodentia, Rhizomyidae), as well as *Tyrannochthonius brevimanus* (2280-3300 m), *Lechyttia maxima* (2350-2650 m), *Cryptocheiridium elgonense* (2650-3200 m), and *Titanatennus palmquisti* (2000-4100 m), all from the well researched Mt Elgon, can be considered as endemics. *T. palmquisti* is found also on

Kilimanjaro and Mt Meru, raising again the question of how the “island” fauna of the Afrotropical mountains (spiders, Chilopods and other groups) might have developed.

Opilionida. Knowledge of the rich montane Afrotropical fauna (at least 66 species living above 2200 m) comes from the studies of Sørensen (1910), Goodnight & Goodnight (1959), Roewer (1913, 1941, 1956), Lawrence (1962), and Kauri (1985). The short footed Cyphophthalmi do not live above 2000 m. The numerous species and genera of the Laniatores are confined mostly to tropical countries, including high in the mountains where they are strikingly predominant. Of the Palpatores, predominant in the Palaearctic Region, in the Afrotropical orear we find only the largest family, Phalangiidae, which contains the bulk of the high altitude opilions, i.e. more than half of all genera and species known within the order occurring above 2200 m.

Among the 66 species of opilionids (46 from Laniatores and 20 from Palpatores, 11 and 6 genera respectively; both relations close to 2:1) recorded above 2200 m (on Kilimanjaro, Mt Kenya, Mt Meru, Mt Elgon, Aberdare, Uluguru, Oldeani, Ruwenzori, Hanang, and Semien), 34 species were found above 3000 m, 26 above 3500 m, 12 above 4000 m, and only two (*Hypoxestus accentuatus*, Assamiidae, and *Rhampsinitus bettoni*, Phalangiidae) above 4500 m.

For an understanding of the sources of the Opilionida fauna of the high mountains of East and Central Africa table 6 may be useful.

Table 6: Distribution of the two suborders of Opilionida in Africa (after Lawrence 1962)

Area	Laniatores		Palpatores	
	Phalangodidae	Assamiidae	Trianenonychidae	Phalangiidae
East Africa	numerous	dominant	absent	numerous
Central Africa (Congo Area)	numerous	dominant	absent	absent
Madagascar	numerous	absent	dominant	absent
Southern Africa	rather numerous	absent	dominant	numerous

In the Afrotropical orear at least 20 genera have been recorded, most of them from the Assamiidae (11 or 55 %), and six from the Phalangiidae (30%).

The endemic genera of Afromontane opilions living between 2200 and 3500 m (usually for several mountains) are : *Monobiantes* (2200 m), *Proconomma* (2400 m), *Abdereca* (3100 m), *Bambereca* (2900 m), *Erecula* (2300 m), *Eusidama* (2400 m), *Metarhabdopygus* (2800 m), *Sesostrellus* (2900 m), *Spinixestus* (2400 m), and *Hindreus* (3300 m). Endemics at or above 3500 m can be found among the members of the genera *Metabiantes*, *Monobiantes*, *Proconomma*, *Aberdereca*, *Bambereca*, *Ereca*, *Erecula*, *Eusidama*, *Hypoxestus*, *Metarhabdopygus*, *Metaereca*, *Randilea*, *Sesostrellus*, *Simienatus*, *Spinixestus*, *Cristina*, *Dacnopilio*, *Guruia*, *Hindreus*, *Odontobunus*, *Rhampsinitus*.

Araneida. Much has been done in the study of Afrotropical spiders, but some of the most important publications were produced by older authors (E. Strand, A. Tullgren, R. de Lessert, H. Fage, E. Simon, L. Berland) and need revision. Newer contributions come from Benoit (1978), Berland (1914, 1920), Bosmans (1977, 1978, 1979, 1981a,b), Bosmans & Jocqué (1983), Denis (1950, 1962), Fage (1940), Lessert (1915-1926), Russel-Smith & Jocqué (1986), Jocqué (1981), Scharff (1992), and Wesolowska (1986).

When we analyze the high-altitude spiders of tropical Africa, we can see that only representatives of the suborder Mygalomorphae (Migidae, Dipluridae) live above 2200 m. Some genera are endemic to Africa (*Mallinella*, *Aberdaria*). The large number of African spiders in the suborder Araneomorphae fit into the general pattern of the Old World (see Introduction).

Some genera living above 2200 m are: *Lepthyphantes*, *Microlinyphia*, *Erigone*, *Asthenargus*, *Oedothorax*, *Meioneta*, *Trichopterna*, *Walckenaeria* (Linyphiidae) and *Heliophanus* (Salticidae).

Altitudes above 3500 m are reached by species belonging to the genera *Pelecopsis* (4930 m) and *Heliophanus*, Salticidae (4650 m), *Araeoncus* (4650 m), *Callitrichia* (4930 m), *Microcyba* (4320 m), *Oreocyba* (4300 m), *Erigone* (4200 m), *Lepthyphantes* (4000 m), *Toschia* (3920 m), *Walckenaeria* (3820 m), *Tybaertiella* (3750 m), *Asthenargus* (3550 m), and *Mallinella*, Zodariidae (3500 m). In Africa no spiders have been found above 5000 m (on the three mountains higher than this).

The family Linyphiidae, the most numerous with 97 species and 30 of the 36 genera, is particularly well studied (Scharff 1992). This family, with *Callitrichia* and *Pelecopsis*, reaches the highest altitudes in Africa. Sixteen genera living above 3000 m belong to the Linyphiidae. Some genera of Linyphiidae have developed many species: *Ctenus* (13), *Microcyba* (12), *Pelecopsis* (12), *Callitrichia* (11), or *Lepthyphantes* (9).

The available data on the Afrotropical spiders are incomplete and unreliable; nevertheless we believe that - as the case is in other montane areas (see later) - in the Afrotropis at an altitude of 2200 m about 50% of all species of spiders belong to Linyphiidae.

Acariformes. Acaridida are not well studied. Some are known from altitudes at or near to 3500 m (family Glycyphagidae with *Glycyphagus domesticus* and family Anoetidae with *Histiostoma telatum*) (André 1945, Mahunka 1982a).

In the mountains of tropical Africa Prostigmata have been studied mainly by Evans and André. Our extensive collections from various mountains are still being studied. The data from the Afrotropical mountains mainly include the families Anystidae, Bdellidae, Erythraeidae, Trombidiidae and Microtrombidiidae. Rhagidiidae (also found in the Himalaya) were collected by us on Kilimanjaro at 3500 m, but are still under study. From the mountains of tropical Africa many genera have been recorded which are either unknown in Europe or not found in the higher zones of European mountains: *Compsothrombium*, *Dinothrombium*, *Dromeothrombium*, *Eutrichothrombium* (Trombidiidae), *Camerotrombidium*, *Enemothrombium* (Microtrombidiidae). On the other hand families, genera and

even species (*Anystis baccharum* L. on Kilimanjaro) are shared with European oréal. The highest record for prostigmatid mites in tropical Africa is at 4200 m (Trombidiidae on Mt Elgon).

Oribatida have been studied by Evans, Balogh, Mahunka, Stary and others. In the Afrotropical oréal at least 19 families have been recorded (see appendix).

The oribatids, reaching or surpassing 3500 m in the Afrotropics, belong to the genera *Liochthonius* (3890 m), *Tectocepheus* (3890 m), *Microtegeus* (4285 m), *Dampfiella* (3890 m), *Amerioppia* (3820 m), *Quadroppia* (3820 m), *Oppia* (4285 m), *Scutovertex* (4438 m), *Incabates?* (3820 m), *Nannerlia* (3890 m), *Zygoribatula* (3810 m), *Schelorbates* (4590 m), *Africorbates* (4590 m), *Ghilarovizetes* (3900 m), and *Oribates* (3810 m). *Schelorbates laevigatus* C.L. Koch was recorded (with questionmark) from Kilimanjaro up to 4590 m. This is also the maximum altitude at which oribatids (and Acari in general) in Africa have been recorded.

Parasitiformes. The suborder Gamasida is not well known, especially in the Afrotropical oréal. Of Ixodida, Neumann (1910) and other authors have recorded the genera *Ixodes* and *Rhipicephalus* in the high mountains of tropical Africa (up to 3500 m on Mt Meru).

Symphyla. This group was studied by Ribaut, Silvestri and Scheller. In equatorial Africa seven species are known to live above 2200 m. The genus *Hanseniella* is dominant in the tropical mountains and is practically the only genus of Symphyla known to live above 3000 m. According to Silvestri (1907) and Scheller (1954), *Hanseniella* lives on Ruwenzori up to 4500 m. *Symphylella vulgaris* is found in Africa (above 2200 m) and in Europe.

Chilopoda. Centipedes were studied mainly by Attems and Ribaut. Scolopendromorpha reach 3500 m (*Cryptops* on Mt Meru and Mt Elgon) and 4000 m (*Scolopendra afra* Mein. on Mt Elgon). Lithobiomorpha are very scarce on the mountains of Central and East Africa. Instead of Lithobiidae we find Henicopidae. The genus *Lamyctes* goes much higher (up to 4200 m on Ruwenzori) than the European Lithobiomorpha. Geophilomorpha: In East Africa one species of *Schendylurus* (Schendyluridae) occurs up to 2210 m. This is a family which East Africa does not share with the other mountains of the Old World, but with South America. Species of *Alloschizotaenia*, Geophilidae, live up to 2800 m, those of *Mecistocephalus*, Mecistocephalidae, reach at least 3900 m (on Nyiragongo).

Diplopoda. This class was studied especially by Attems (1909, 1939), Brölemann (1920), and Mauriès & Heymer (1996). At least four orders live in tropical Africa above 2200 m: Polyxenida, Stemmiulida, Spirostreptida and Polydesmida. The tiny Polyxenida are represented in tropical Africa by one family (Polyxenidae) up to 2740 m (Mt Elgon). The family Stemmiulidae (Stemmiulida) reach 3500 m on Mt Meru, the Odontopygidae (Spirostreptida) reach 3000 m on Kilimanjaro. Polydesmida are represented in the Afromontane environment by the families Fuhrmannodesmidae (*Elgonicola jeanneli* Attems up to 3500 m on Mt Elgon, and *Sphaeroparia petarberoni* Mauriès et Heymer up to 4200 m on Ruwenzori) and Oxydesmidae (up to 3000 m on Kilimanjaro).

Comparison between the Isopoda, Arachnida and Myriapoda of the Palaearctic and the Palaetropical mountain systems

IAM in the Atlas and the mountains of tropical Africa

None of the many Afrotropical species, genera and even families of IAM is known to live in the orals of the Atlas (Alderweireldt & Jocqué 1992, Denis 1961, 1967, Lépiney 1939, Verhoeff 1937, 1938 a,b). The montane IAM of the Atlas are of clearly Palaearctic type, which agree with the findings of other groups of animals and plants.

IAM in the European orals and in the mountains of tropical Africa

Isopoda. If we compare the high mountain Isopods of Europe and of tropical Africa, we can see that between the 24 species in Europe and the 66 species in tropical Africa living higher than 2200 m there are no species in common. Of the 10 genera in Europe and the 35 in tropical Africa there are no genera in common. At the family level there is some overlap at this altitude: just two of the seven families living in Europe and the five in Africa are shared by the two continents (Porcellionidae and Oniscidae).

In Europe the highest altitude is reached by representatives of the genus *Porcellio* (3300 m in Sierra Nevada). The family Porcellionidae is not very numerous in the montane Afrotropis. The highest occurring species belong to *Uramba* at 2500 m and *Thermocellio* at 2200 m – in the zone of tropical montane forests. The numerous Eubelidae (up to 4600 m), Philosciidae (up to 3700 m) and Armadillidae (up to 3100 m), so typical of the Afrotropis, are absent from the high mountains of Europe; Eubelidae do not live in Europe at all.

Table 7: Comparison of typical families of Isopoda between European and Afrotropical orals

European orals	Afrotropical orals
Porcellionidae	Porcellionidae
Oniscidae	Oniscidae
Trichoniscidae	Philosciidae
Mesoniscidae	Eubelidae
Buddelundiellidae	Armadillidae
Trachelipodidae	
Armadillidiidae	

Pseudoscorpionida. Only 12 species of Pseudoscorpionida, belonging to 3 genera (*Chthonius*, *Neobisium*² and *Allochernes*) are known from the European orals

² One exception is the European species *Neobisium muscorum* (= *N. carcinoides*), recorded by Mahnert (1981) on the basis of tritonymphs from Aberdare in Kenya (3203 m), the first representative of *Neobisium* in Africa south of the Sahara. In the extensive collections of Mahnert from African mountains, as well as in the collections of the older specialists (publications of M. Beier), we could not find *Neobisium*, so the authenticity and the autochthonous character of this species is doubtful. This is why we do not consider this record in our zoogeographical analysis.

(without the Caucasus). These genera are absent from the mountains of equatorial Africa.

In the mountains of equatorial Africa all three European families are present, but also eight families more, three of which (Lechytiidae, Tridenchthoniidae and Ideoroncidae) do not live in Europe at all. Except the doubtful *Neobisium*, none of the remaining Afrotropical genera occurs in the European oreals. Only two of the genera (*Withius* and *Apocheiridium*) live on the European continent at all.

Table 8: Comparison of families and genera of Pseudoscorpionida in the oreals of Europe and the Afrotropis

Europe	Afrotropis
Chthoniidae	Chthoniidae
Chthonius - up to 3030 m	Tyrannochthonius - up to 2900 m
Neobisiidae	Neobisiidae
Neobisium - up to 3600 m	Microbisium - up to 3300 m
Chernetidae	(Neobisium - up to 3203 m)
Allochernes - up to 2600 m	Chernetidae
	Caffrowithius - up to 3300 m
	Nudochernes - up to 3700 m
	Lechytiidae
	Lechytia - up to 2900 m
	Tridenchthoniidae
	Compsaditha - up to 2300 m
	Verrucadithella - up to 3200 m
	Geogarypidae
	Afrogarypus - up to 2900 m
	Ideoroncidae
	Negroroncus - up to 2250 m
	Cheiridiidae
	Apocheiridium - up to 2300 m
	Cryptocheiridium - up to 3200 m
	Atemnidae
	Cyclatemnus - up to 3000 m
	Micratemnus - up to 2200 m
	Paratemnoides - up to 3050 m
	Titanatemnus - up to 4100 m
	Cheliferidae
	Hansenius - up to 2250 m
	Microchelifer - up to 2700 m
	Withiidae
	Ectromachernes - up to 3000 m
	Stenowithius - up to 2180 m
	Trichotowithius - up to 3000 m
	Withius - up to 3500

Opilionida. All high-mountain harvestmen in Europe belong to five families of the Palpatores (28 species above 2200 m). In the mountains of equatorial Africa above 2200 m, 66 species of Opilionida (46 Laniatores and 20 Palpatores) have been recorded. In Europe only two species live above 3000 m (both in the genus *Mitopus*), in equatorial Africa 34.

Araneida. Out of the 18 genera of spiders, known in the Afrotropical oréal above 3000 m, more than half are also represented in similar habitats in Europe (*Lepthyphantes*, *Microlinyphia*, *Erigone*, *Asthenargus*, *Araeoncus*, *Ceratinopsis*, *Pelecopsis*, *Meioneta*, *Walckenaeria*, *Heliophanus*). From eight genera known above 4000 m, five (*Lepthyphantes*, *Erigone*, *Araeoncus*, *Pelecopsis*, *Heliophanus*) are also inhabitants of the higher parts of European mountains.

Acariformes. The mites of the suborder Acaridida are not adequately studied in both areas. The genus *Histiostoma* (Anoetidae) is present both in European and Afrotropical mountains. In Europe and especially in the Alps Prostigmata are better known (over 2200 m with at least 20 families, 35 genera and more than 100 species, excluding the strict parasites such as Myobiidae, Listrophoroidea, etc.). This group is less well known in the Afrotropical oréal. Families, genera and even species (*Anystis baccarum* L.) are shared with the European oréal. The highest record for prostigmatid mites in Europe is at 3774 m (Bdellidae in the Alps), in tropical Africa at 4200 m (Trombididae on Mt Elgon). In Europe, many genera recorded on the mountains of tropical Africa are either unknown or are found only in the lower regions.

We have already considerable information on the representatives of Oribatida in the oreals of Europe and tropical Africa. Most of the families in the Afrotropical oréal live also in the European mountains. Many genera are also shared (*Liochthonius*, *Brachychthonius*, *Heminothrus*, *Nothrus*, *Nanhermannia*, *Scheloribates*, *Ceratozetes*, *Galumna*, *Tectocephus*, *Suctobelba*, *Oppia*, *Quadropia*, *Rhysotritia*). *Scheloribates laevigatus* C.L. Koch occurs in the Alps up to 2700 m.

Parasitiformes. The suborder Gamasida is not well known in both regions. The other suborder, Ixodida, is represented in both with different species of the genus *Ixodes*.

Symphyla. Both families of Symphyla live in both regions. In Europe, seven species are known above 2200 m, in equatorial Africa also seven. The two regions even share one species - *Symphylella vulgaris*. All other Afrotropical Symphyla belong to the genus *Hanseniella*, represented also in Europe but only by a small number of lowland species. In the Afrotropical oréal the genera *Geophilella* and *Scutigerebella* have not been found, but they are known from some European mountains.

Chilopoda. In Europe, Geophilomorpha reach 2900 m (*Geophilus*) and Scolopendromorpha 2700 m (*Scolopendra*, both in the Sierra Nevada). Scutigereomorpha do not live in the higher parts of the European mountains. Lithobiomorpha (family Lithobiidae) is represented by the genera *Eupolybothrus* (up to 2500 m) and *Lithobius* (up to 2914 m), in total by at least 20 species.

In the Afrotropical oréal Geophilomorpha reach at least 3900 m (*Mecistocephalus* on Nyiragongo), and Scolopendromorpha 3500 m (*Cryptops*, *Lamnonyx* on Mt Meru and Mt Elgon). Instead of Lithobiidae (Lithobiomorpha) we find

Henicopidae in the Afrotropical orear. The genus *Lamycetes* occurs much higher than the European Lithobiomorpha (4000 m).

Diplopoda. Of the 13 orders of Diplopoda living in high-altitude environments of the Old World, six live in the European and four in the Afrotropical orear (table 9).

Table 9: Comparison of the occurrence of orders (and families) of Diplopoda in the oreals of Europe and Africa

European orear	African orear
Polyxenida (Polyxenidae)	Polyxenida (Polyxenidae)
Glomerida	–
Craspedosomatida	–
Julida	–
Chordeumatida	–
–	Stemmiulida
–	Spirostreptida
Polydesmida (Polydesmidae)	Polydesmida (Fuhrmannodesmidae, Paradoxosomatidae)

We can see that at the level of orders there are considerable differences between the two areas. Only two orders - the Polyxenida and Polydesmida - and one family - Polyxenidae - are shared.

IAM in the Himalaya and mountains of tropical Africa

The Himalaya is much higher and is situated farther north than the mountains of tropical Africa. Nevertheless, some IAM reach higher altitudes in the Himalaya (over 5000 and even 6000 m) than in the African orear. The Himalaya has a dual zoogeographical character: it belongs partly to the Palaetropical realm, of which the mountains of tropical Africa are also a part, but their northern slopes form the southern limit of the Holarctic.

Table 10: Comparison of the families of Isopoda from the Himalaya and Afrotropical mountains

Himalaya above 2200 m	Afrotropics above 2200 m
Philosciidae	Philosciidae
Armadillidae	Armadillidae
Porcellionidae	Porcellionidae
Oniscidae	Oniscidae
Trachelipodidae	Eubelidae

Isopoda. Only nine species of terrestrial Isopoda, belonging to five families, have been recorded so far from the Himalaya from altitudes over 2200 m. In the Afrotropical oréal their number is much higher: 66 species in 5 families. Of these five families four are shared by the two regions. The family Eubelidae in Africa is replaced by the Trachelipodidae in the Himalaya (see table 10). None of the five genera of woodlice in the high Himalaya and the 35 genera in the mountains of tropical Africa occurs in both regions.

Pseudoscorpionida. In the Himalaya above 2200 m, 30 species of pseudoscorpions have been found, 17 species above 3000 m, 7 above 3500 m, and 2 above 4000 m. The species living higher than 2200 m belong to 20 genera and 12 families. In the mountains of tropical Africa above 2200 m, 56 species in 25 genera and 13 families are known (without the doubtful finding of *Neobisium* - see footnote p.166). There is a considerable similarity in the number of taxa of all ranks. In the Himalaya, the family Hyidae (the highest) is additional, in the Afrotropical mountains the Ideoroncidae. Both mountain systems share 10 families and 5 genera above 2200 m: *Tyrannochthonius*, *Lechytia*, *Apocheiridium*, *Calocheiridius* and *Withius*. There are no species in common. In the Himalaya, pseudoscorpions have been recorded up to 5000 m (*Stenohya*), and in the Afrotropical oréal up to 4100 m (*Titanatemnus*).

Table 11: Decrease in number of species of Pseudoscorpionida with altitude in the Himalaya and the mountains of the Afrotropics

	Himalaya	Afrotropics
> 2200 m	30	56
> 3000 m	17	22
> 3500 m	7	6
> 4000 m	2	1

Opilionida. As already said, the opilionid fauna of the Himalaya reflects the dual zoogeographic character of this mountain system. In the higher parts of the Himalaya both suborders Laniatores and Palpatores (the last suborder being predominant) are present. In the Himalayan opilionids above 2200 m (including four species found up to 2150 m) the ratio of the genera of Laniatores:Palpatores is 9:21, and of species 29:58 (in both cases approximately 1:2). For comparison: in the mountains of Central and equatorial East Africa above 2200 m, the ratio of genera is 11:5, and of species 46:20. The ratio is just the opposite.

In the Afrotropical oréal, 26 opilionid species (out of 66) have been found above 3500 m, 12 above 4000 m and only two (*Hypoxestus accentuatus*, Assamiidae, and *Rhampsinitus bettoni*, Phalangiidae) above 4500 m. In the Himalaya above 2200 m, at least 87 opilionid species are known, 45 above 3000 m, 15 above 3500 m, seven above 4000 m and two above 4500 m (*Himalphalangium palpale*, Phalangiidae, and *Sabacon* sp., Sabaconidae, which occurs even above 5000 m). In the mountains of tropical Africa above 2200 m, three families of Opilionida (Assamiidae, Biantidae, Phalangiidae) are found, and seven in the Himalaya. All high-altitude

African families are also present in the high Himalaya, but four additional families occur (Oncopodidae, Sabaconidae, Phalangodidae, Sclerosomatidae). In the Afrotropical oréal at least 20 genera have been recorded, 11 (55%) of Assamiidae and six (30%) of Phalangiidae, more typical of the Holarctic realm. In the high Himalaya, Martens, Suzuki and other specialists have found representatives of at least 30 genera above 2200 m, 6 (20%) of Assamiidae and 18 (60%) of Phalangiidae. There are no genera in common between the two mountain systems.

Araneida. There are some differences between the Himalayan and the Afrotropical oreals in families and even in suborders. In the Afrotropical oréal (up to 2500 m) representatives of Mygalomorphae occur that are absent in the Himalaya above 2200 m. Here, only species of the suborder Araneomorphae are known (Anapidae, Tetrablemmidae, Sicariidae, Salticidae, etc). In both areas the family Linyphiidae dominates. Both systems also share some genera belonging to this family (*Lepthyphantes*, *Erigone*, *Asthenargus*, *Walckenaeria*, *Oedothorax*) which also occur in the European oréal. Some genera have developed many species in the high Himalaya: *Lepthyphantes* (19), *Yaginumaella* (14), *Xysticus* (9), and *Pardosa* (8). But there are no species in common between the Himalaya and Central Africa.

We found that four families of spiders in the Old World form the highest associations, inhabiting the regions above 5000 m: Lycosidae, Salticidae, Linyphiidae and Gnaphosidae. In the Himalaya above 3500 m, we find 18 genera, the highest at 6100 m. In Africa no spiders have been found above 5000 m (in the three mountains overpassing this altitude).

Acariformes. No information exists on Himalayan Trombidiidae, but the other recorded Prostigmata in both areas are completely different. Rhagidiidae have been collected by us on Kilimanjaro at 3500 m, but are still under study and it is not possible to compare them with the five species of five genera found in the Himalaya at 3900 m (Zacharda & Daniel 1987).

Oribatida. Almost all families and genera, recorded from the high Himalaya (above 2200 m) are also known from the higher mountains of tropical Africa. In the Himalaya a few species have been recorded from this altitude, mostly by Aoki, Piffel, Sheals, Travé, Mahunka and other authors. Janetschek (1990) mentions many species - identified only up to the genus, found during his expedition up to 5800 m - that are some of the highest in the world. The genera, however, are widespread and are present also in the European mountains (*Liochthonius*, *Hermannia*, *Belba*, *Oribatula*, *Scheloribates*, *Trichoribates*, *Oribatella*, *Ceratoppia*, *Tectocephus*, and *Suctobelba*).

Parasitiformes. The suborder Gamasida is not well known in both regions. The suborder Ixodida reaches 5488 m in the Himalaya (*Ixodes berlessei* Birula, the highest locality for Ixodida and Parasitiformes in the world). At least six species of the genus *Ixodes* in the Himalaya live above 3600 m. In the Himalaya *Haemaphysalis aponommoides* Warburton also occurs up to 4880 m, as does the endemic genus *Anomalohimalaya*. In tropical Africa *Ixodes* (with different species) and *Rhipicephalus* reach considerable altitudes (up to 3500 m).

Symphyla. The two families in the class Symphyla and the genus *Hanseniella* are shared by the Himalaya and the mountains of equatorial Africa. In the high Himalaya only 1-2 species of Symphyla have been recorded (up to 4900 m), as opposed to seven species in the higher parts of equatorial Africa (up to 4500 m).

Chilopoda.

Scutigermorpha. Not yet identified scutigermorphs have been collected by us in Nepal up to 4250 m. There is no information concerning this order in the high-altitude tropical Africa.

Lithobiomorpha. The centipedes of this order are widespread in the Himalaya and known up to 5545 m (*Lithobius hirsutipes khumbensis*). In these mountains above 2200 m at least ten species have been found, all belonging to Lithobiidae (*Lithobius* with two species). The family Lithobiidae and genus *Lithobius* are known from the High Atlas, but are absent from the Afrotropical mountains. There we find (up to 4000 m on Mt Kenya) two species of the genus *Lamycetes* (family Henicopidae), which is unknown in the high Himalaya. The difference between the two oreals in the Lithobiomorpha is at the family level.

Geophilomorpha. As in the Lithobiomorpha, the difference here also lies at the family level: in the Himalaya at least two species of *Tygarrup* (Mecistocephalidae) occur, in East Africa one species of *Schendylurus* (Schendyluridae).

Scolopendromorpha. Several Scolopendromorpha (Scolopendridae) live in the high Himalaya above 2200 m (*Cryptops* up to 4500 m, *Otostigmus* up to 3000 m, *Ethmostigmus* up to 2700 m and *Rhysida* up to 3400 m). That means that only *Cryptops* is shared by the oreals of the Himalaya and Central Africa.

Diplopoda. In the last two decades the Diplopoda fauna in the Himalaya has become one of the best known in the world, mainly because of the intensive field work of J. Martens and the research of Golovatch, Mauriès, Enghoff, Shear and

Table 12: Comparison of the orders and families of Diplopoda between the Himalayan and Afrotropical areal

	Himalaya	Africa
Order Spirostreptida	Harpagophoridae	Odontopygidae
Order Polydesmida	Fuhrmannodesmidae Paradoxosomatidae Polydesmidae Opisotretidae	Fuhrmannodesmidae Paradoxosomatidae Oxydesmidae
Order Polyxenida	Polyxenidae	Polyxenidae

other specialists. The two regions share three orders: Polyxenida, Spirostreptida and Polydesmida, but only three families (Polyxenidae, Fuhrmannodesmidae, and Paradoxosomatidae) and not a single genus (table 12).

At least five genera in the family Fuhrmannodesmidae live in the Himalaya above 2200 m, while on Ruwenzori in the Afrotropical or the genus *Sphaeroparia* reaches 4200 m (*S. petarberoni* Mauriès et Heymer).

IAM in the mountains of tropical Africa and Central Asia

The mountains of Central Asia (Afghanistan, Pakistan, Hindu Kush, Karakorum, Pamir, Tien Shan, Kunlun, and Tibet - from the border between Iran and Afghanistan to 120° E) are situated more to the north and are higher than the mountains of tropical Africa (which do not reach 6000 m). The two systems have a different vertical zonation, origin, climate and vegetation. They also belong to different zoogeographical regions and even realms, and their faunas have been isolated from each other at least since the Quaternary.

Isopoda. From the mountains of Central Asia only ten species of Isopoda have been recorded above 2200 m, belonging to three families. The two areas in question share two families: Porcellionidae and Armadillidae. In the mountains of tropical Africa the family Eubelidae dominates, but does not occur in Central Asia. The Central Asian mountains share the family Trachelipodidae with Europe and the Himalaya. None of the four genera in the Central Asian or the 35 genera in Afrotropical mountains is common to both. The arid mountains of Central Asia are characterized by genera like *Protracheoniscus* and *Desertoniscus* (as high as 4725 m), the Afrotropical or the more hygrophilous representatives of Eubelidae, Philosciidae, etc. (up to 4600 m).

Pseudoscorpionida. At least 12 species in eight families have been recorded from Central Asia above 2200 m, including 11 above 3000 m and four above 3500 m. From the or of tropical Africa over 2200 m, 28 species of Pseudoscorpionida have been recorded, belonging to 21 genera and 11 families (up to 4100 m). The highest Central Asian records within the Neobisiidae are of *Bisetocreagris kaznakovi* (Red.) (Tibet 4810 m), and within the Cheliferidae *Dactylochelifer brachialis* Beier (Karakorum 4200 m), *Gobichelifer chelanops* (Red.) (Karakorum 3650 m) and "*Chelifer*" *baltistanus* di Cap. (Karakorum 3950 m). All families of pseudoscorpions from montane Central Asia live also in the high mountains of tropical Africa; of the African families, the Lechytiidae, Tridenchthoniidae and Withiidae are not represented in Central Asia above 2200 m. There are no genera in common between the two areas.

Opilionida. Few species of Opilionida are known to live in the vast arid mountains of Central Asia. This fauna is much poorer than the Himalayan or the Afrotropical.

They all belong to the suborder Palpatores and mainly to the family Phalangidae s.lat. (one species belongs to Sclerosomatidae). The highest species is *Homolophus nordenskioeldi*, living at up to 5600 m (a world record for Opilionida). Representatives of the genera *Diabunus*, *Egaenus*, *Opilio*(?) and *Phalangium*(?) live above 3500 m. These data are rather fragmentary and after research in some remote corners of Tibet with Indomalayan influence the picture is likely to change.

For the moment there are no Opilionid genera in common between the Afrotropical and the Central Asian orals.

Araneida. In Central Asia above 2200 m more than 180 species of spider have been found, belonging to 18 families, but only four families contain at least 148 of these species: Linyphiidae (87), Gnaphosidae (22), Salticidae (19) and Lycosidae (20). The 88 species of the Linyphiidae belong to 36 genera (in the Afrotropical oral there are 97 species in 30 genera). The figures are quite close. We have already pointed to the amazing coincidence in the percentage of high-altitude Linyphiidae versus the other spiders in the high Alps (51,2%) and in the mountains of Central Asia (51,8%). Nine genera (probably more) are common to the two areas above 2200 m: *Lepthyphantes*, *Microlinyphia*, *Erigone*, *Asthenargus*, *Oedothorax*, *Meioneta*, *Trichopterna*, *Walckenaeria* (Linyphiidae) and *Heliophanus* (Salticidae).

We mentioned already that in tropical Africa more than half of the 18 genera of spiders living above 3000 m are also represented in the oral of Europe. Of the genera living above 3500 m (38 in Central Asia, 14 in the Afrotropical oral) four are shared, of those above 4000 m (8 in Africa, 26 in Central Asia) three are shared, and above 4500 m only *Erigone* and *Heliophanus* live in both areas. The four shared genera above 3500 m are:

Heliophanus (Salticidae): 4600 m (Central Asia), 4650 m (tropical Africa)

Erigone (Linyphiidae): 4950 m (Central Asia), 4200 m (tropical Africa)

Lepthyphantes (Linyphiidae): 4250 m (Central Asia), 4000 m (tropical Africa)

Pardosa (Lycosidae): 5170 m (Central Asia), 3700 m (tropical Africa).

Acariformes. The suborder Oribatida deserves special attention, as there is reliable information about these important mites in both regions. There are a number of common families: of the 20 families in the Afrotropical oral and the 35 in Central Asia, 12 are shared, but many others may also be in common since they occur in one of the regions but have so far been recorded only at lower altitudes. There are also some genera in common (*Liochthonius*, *Heminothrus*, *Nanhermannia*, *Tectocephus*, *Amerioppia*, *Quadroppia*, *Oppia*, *Scutovertex*, *Zygoribatula*, *Scheloribates*) but no species.

In the mountains of Central Asia an altitude of 3500 m is reached by the genera *Hypochthonius*, *Liochthonius*, *Heminothrus*, *Nothrus*, *Scutovertex*, *Zygoribatula*, *Gerloubia*, *Scheloribates*, *Ceratozetella*, *Diapterobates*, *Punctoribates*, *Eupelops*, *Unduloribates*, *Suctobelbella*, and *Novosuctobelba*, that of 5000 m by *Tectocephus*, *Oribotritia*, *Oribatella*, and *Sphaerobates*.

In this (clearly incomplete) list of 19 Central Asian montane genera we find five living in both oreals: *Liochthonius*, *Tectocephus*, *Scutovertex*, *Zygoribatula*, and *Scheloribates*. The limit of 3500 m for many of the Central Asian genera is an artificial one, because this was the upper limit of the research carried out by Maria Hammer in the Hindu Kush. In the Himalaya, oribatids have been recorded up to 6100 m, which may be true for Central Asia too. For the other Acari, *Ixodes* is the shared genus (up to 3600 m in Tien Shan, up to 3500 m on Mt Meru).

Symphyla. So far no specimens of this class have been recorded from Central Asia.

Chilopoda.

Lithobiomorpha. As in Europe and the Himalaya, in Central Asia representatives of the genus *Lithobius* (Lithobiidae up to 4300 m) dominate, and they do not occur in the Afrotropical oréal. In Tajikistan we found another genus of the family Lithobiidae: *Hessebius*, as high as 4500 m. In tropical Africa the litho-biomorphs are represented by the family Henicopidae (*Lamyctes* up to 3500 m).

In the **Scolopendromorpha** one genus is shared by the two oreals - *Scolopendra* (in Central Asia up to 2700 m, in tropical Africa up to 2710 m). This is the only genus of Scolopendromorpha collected in Central Asia so far.

The order **Geophilomorpha** in Central Asia is represented by two families (Geophilidae up to 2820 m in Afghanistan and Mecistocephalidae up to 3500 m in Tibet). They live also in the Afrotropical oréal, but the genera are different.

Scutigeromorpha. Verhoeff has described one species of the genus *Thereuopoda* from Central Asia (3100 m); they are unknown in the oréal of tropical Africa.

Diplopoda. Central Asia, and especially its high and arid parts, are among the poorest regions for Diplopoda in the world. According to Golovatch, in the deserts of Central Asia huge regions exist where this forest-dwellers are absent. The few genera we know of are close to the Himalayan fauna and have nothing in common with the rich diplopod fauna living in the Central African mountains.

Discussion

The comparison between the non-insect arthropod faunas of the montane Afrotropics and the oreals of Eurasia reveals many agreements but more differences. If we exclude the case of *Neobisium carcinoides* (see footnote p. 166), there are no shared species. Table 13 presents what we see in the genera.

Obviously the mutuality depends largely on the mobility of the animals. In groups with low mobility (Isopoda, Opilionida, Diplopoda) there are no common genera. Some others (Araneida, Acariformes, Parasitiformes) are more widespread. In the case of Araneida the higher mobility may be caused by ballooning, in the parasitiform mites the mobility of the hosts is obviously the reason for their extension.

But we know many examples which do not fit in this scheme. According to Scharff (1992), 14 linyphiid spiders (Araneida) are endemic to the Afroalpine region. He quotes: "The high degree of endemism among forest linyphiid species on nearby mountains in eastern Tanzania does not support a theory of common or

Table 13: Number of genera in different taxa in the montane Afrotropis (above 3500 m) and those shared with in the corresponding altitudes of Eurasia

Class or order	no. in the Afrotropis	shared genera in Eurasia
Isopoda	10	0
Scorpionida	1	0
Pseudoscorpionida	4	2
Opilionida	9	0
Araneida	18	13
Acariformes	21	18
Parasitiformes	4	4
Symphyla	1	1
Chilopoda	5	2
Diplopoda	3	0

occasional contact between the faunas as a result of ballooning". A mite of the family Bdellidae (Acariformes, Prostigmata) is not more mobile than a spider, but we can see that *Bdella*, *Erythraeus* and other Prostigmata can be found in all or most continents. A *Pardosa* spider (Araneida, Lycosidae) is not more mobile than any of the Opilionida, but the harvestmen on African mountains are largely endemic to the continent whereas those lycosids are widespread. Most genera of Oribatida (Acariformes) are also widespread although they have low mobility. These patterns obviously depend on other factors, such as age of the group, ecological plasticity, type of speciation, etc.

The distribution of some families, e.g. Eubelidae (Isopoda), Assamiidae and Biantidae (Opilionida), is palaeotropical or pantropical. Their genera, however, are entirely Afrotropical and have evolved in Africa. Very few of them are confined to the montane regions.

Fage (1940) noted that the separate high mountain massifs in tropical Africa (Kilimanjaro, Mt Kenya, Mt Elgon, Ruwenzori and others), rising like islands amidst the dry and hot savanna, share many species of spiders. It is obvious that their establishment must have taken place under quite different climatic conditions, when the montane environment was more widespread. An active exchange at present is impossible.

According to Scharff (1992) the idea of Fage (1940) is not verified by the actual data: "It is a general trend that the different mountains harbour different linyphiid species". In the opilionids, however, we see that many of them live on two or more mountain massifs, with the reservation that until now only some of the many high mountains have been sufficiently investigated.

References

A selection of papers on the non-insect arthropods in tropical Africa above 3500 m and papers used in the text:

- Alderweireldt, M. & R. Jocqué (1992): A contribution to the knowledge of the wolf spider fauna of Morocco: new species and new records (Araneae: Lycosidae). – *Phegea* 20: 15-119.
- Alluaud, Ch. (1908): Les coléoptères de la faune alpine du Kilimandjaro avec notes sur la faune du Mont Meru. – *Ann. Soc. ent. France* 77: 21-32.
- Alluaud, Ch. & R. Jeannel (1912): Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912). Liste des Stations, 24 p. – Limoges et Paris.
- André, M. (1936): Descriptions de plusieurs Microthrombidium de l'Afrique Orientale (Mission de l'Omo, 1932-1933). – *Bull. Mus. nat. Hist. nat. Paris*, 2e s. 8(5): 406-422.
- André, M. (1938): Mission scientifique de l'Omo.- *Mém. Mus. nat. Hist. nat. Paris, Zoologie*, 37(4): 212-254.
- André, M. (1945): Mission scientifique de l'Omo, VI. 57. Faune des terriers des rats-taupes. XI. Acariens. – *Mém. Mus. nat. Hist. nat. NS* 19(1): 199-210.
- André, M. (1957): Contribution à l'Etude des Thrombidions du Congo Belge. – *Rev. Zool. Bot. Afr.* 56(3-4): 301-344.
- André, M. (1965): LXXXVI – Acari Thrombidiidae. Mission zoologique de l'I.R.S.A.C. en Afrique orientale. (P. Basilewsky et N. Leleup, 1957).- *Ann. Mus. Roy. Afr. Centr.*, 8, Zool. 138: 65-75.
- Attems, C.G. (1909): Myriopoda. – In: *Wissenschaftliche Ergebnisse der Kilimanjaro-Meru Expedition* (ed. Sjöstedt, Y.). – Stockholm, 3: 1-64.
- Attems, C.G. (1937): Chilopoden und Symphylen des Belgischen Congo. – *Rev. Zool. Bot. Afr.* 29(3): 317-332.
- Attems, C.G. (1939): Myriopoda. – In: *Mission Scientifique de l'Omo*, V. – *Mém. Mus. Nat. Hist. nat.*, NS, 5(55): 303-318.
- Balogh, J. (1966): On some oribatid mites from Tshad and East Africa collected by Prof. H. Franz, Vienna. – *Opusc. Zool. Budapest* 6(1): 69-77.
- Barnard, K. H. (1940): XXXVI. Entomological Expedition to Abyssinia, 1926-7: Woodlice collected by Mr. J. Omer-Cooper. – *Ann. Mag. nat. Hist.* (1) 6: 355-366.
- Beier, M. (1944). Über Pseudoscorpioniden aus Ostafrika. – *Eos, Madrid* 20: 173 – 212.
- Beier, M. (1951): On some Pseudoscorpioidea from Kilimanjaro. – *Ann. Mag. Nat. Hist.* 12(4): 606-609.
- Beier, M. (1955): Pseudoscorpionide, gesammelt während der schwedischen Expeditionen nach Ostafrika 1937-38 und 1948. – *Ark. Zool.*, ser. 2, 25: 527-558.
- Beier, M. (1959): Pseudoscorpione aus dem Belgischen Congo gesammelt von Herrn N. Leleup. – *Ann. Mus. Congo Belge, Sci. Zool.* 72: 5-69.

- Beier, M. (1962): Pseudoscorpionidea. In: Mission Zoologique de l'I.R.S.A.C. en Afrique orientale VIII. – Ann. Mus. Roy. Afrique. Centr. Tervuren, ser. 8, Sci. Zool. 107: 9-37.
- Benoit, P. L. G. (1978): Hahniidae du Mont Kenya (Araneae). Scientific Report of the Belgian Mt. Kenya Bio-Expedition, 1975, No 16. – Rev. Zool. afr. 92(3): 609-621.
- Berland, L. (1914): Arachnida III: Araneae (Ire partie). – Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912), Résultats scientifiques: 37-94.
- Berland, L. (1920): Arachnides IV: Araneae (2e partie). – Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912), Résultats scientifiques: 95-180.
- Bosmans, R. (1977): Scientific Report of the Belgian Mt. Kenya Bio-Expedition No 3. Spiders of the subfamily Erigoninae. – Rev. Zool. afr. 91(2): 449-472.
- Bosmans, R. (1978): Description of four new *Lepthyphantes* species from Africa, with a redescription of *L. biseriatus* Simon & Fage and *L. tropicalis* Tullgren. – Bull. Br. arachnol. Soc. 4(6): 258-274.
- Bosmans, R. (1979): Scientific report of the Belgian Mt. Kenya bio-expedition No 17. Spiders of the subfamily Linyphiinae from Mount Kenya (Araneae-Linyphiidae). – Rev. Zool. afr. 93(1): 53-100.
- Bosmans, R. (1981a): Scientific Report of the Belgian Mt. Cameroon Expedition 1981. I. Situation of the collecting sites on the altitudinal gradient. Description of *Hahniolepis* n.sp. – Rev. Zool. afr. 96(3): 670-682.
- Bosmans, R. (1981b): Études sur les Hahniidae (Araneae) africains II. Les espèces du genre *Hahniolepis* de la collection Simon. – Bull. Mus. natn. Hist. nat., Paris, 4e sér., sect. A, 1: 203-211.
- Bosmans, R. (1985): Les genres *Troglohyphantes* Joseph et *Lepthyphantes* Menge en Afrique du Nord (Araneae, Linyphiidae). Études sur les Linyphiidae nord-africaines, III. – Rev. Arachnol. 6(4): 135-178.
- Bosmans, R. & R. Jocqué (1983): Scientific report of the Belgian Mount Cameroon expedition 1981. No 9. Family Linyphiidae (Araneae). – Rev. Zool. afr. 97(3): 581-617.
- Bosmans, R. & E. Thijs (1980): Spiders of the family Hahniidae from Mount Kenya. Scientific report of the Belgian Mt. Kenya bio-expedition no 20. – Revue Zool. afr. 94(3): 559-569.
- Brölemann, H. W. (1920): Myriapodes III Diplopoda. – In: Voyage de Ch. Alluaud et R. Jeannel en Afrique orientale (1911-1912). – Rés. Sci.: 49 – 298.
- Budde-Lund, G. (1910): Crustacea. Isopoda. – In: Wissenschaftliche Ergebnisse der Kilimanjaro-Meru Expedition (ed. Sjöstedt, Y.) 3: 3-20.
- Černík, A. & J. Sekyra (1969): Zemepis velehor. – Academia, Praha.
- Coe, M. J. (1967): The ecology of the Alpine zone of Mount Kenya. – Monograph. Biol. 17: VIII + 136 p.

- Coe, M.J. (1989): Biogeographical affinities of the high mountains of tropical Africa. – In: Quaternary and environmental research on East African mountains (ed. Mahaney, W.C.) – Rotterdam: 257-278.
- De Lattin, G. (1967): Grundriss der Zoogeographie. – Gustav Fischer Verlag, Jena.
- Denis, J. (1950): Spiders from East and Central African mountains collected by Dr. George Salt. – Proc. zool. Soc., London 120: 497-502.
- Denis, J. (1961): Notes d'aranéologie marocaine. IX. Les Araignées du Maroc. I. Orthognatha et Haplogynae. – Soc. Sci. Nat. Phys. Maroc 41: 141 - 167.
- Denis, J. (1962): Notes sur les Erigonides. XX. Erigonides d'Afrique orientale avec quelques remarques sur les Erigonides éthiopiens. – Rev. Zool. Bot. Afr. 65(3-4): 169-203.
- Denis, J. (1967): Notes d'Aranéologie marocaine. X. Les Erigonides du Maroc. – Bull. Soc. Sci. Nat. Phys. Maroc 47: 137-164.
- Evans, G.O. (1953): On a collection of Acari from Kilimanjaro. – Ann. Mag. nat. Hist. 12(6): 258-281.
- Fage, L. (1940): Le peuplement en Arachnides des hauts massifs montagneux de l'Afrique Orientale. – VI-e Congrès intern. Entom., 1935, 2: 487-491.
- Ferrara, F. & S. Taiti (1984): New species and records of Philosciidae (Terrestrial & Isopods) from Eastern Africa. – Rev. Zool. afr. 98(2): 293-307.
- Franz, H. (1979): Ökologie der Hochgebirge. – Ulmer Verlag, Stuttgart, 495 p.
- Fries, R.E. & T.C.E. Fries (1948): Phytogeographical researches on Mount Kenya and Mt. Aberdare, British East Africa. – K. Svenska Vetensk. Akad. Handl. 111, 25(5).
- Goodnight, C.J. & M.L. Goodnight (1959): Report on a collection of Opilionids from East Africa. – Ark. Zool. 12(15): 197-222.
- Hauman, L. (1955): La "région afro-alpine" en phytogéographie centro-africaine. – Webbia 11: 467-469.
- Hedberg, O. (1951): Vegetation belts of the east African mountains. – Svensk. Bot. Tidskr. 45: 140-202.
- Hedberg, O. (1965): Afro-alpine flora elements. – Webbia 19: 519-529.
- Hingston, R.W.G. (1925): Animal life at high altitudes. – Geogr. J. 65: 185-198.
- Holm, A. (1962): The spider fauna of the East African mountains. – Zool. Bidr., Uppsala 35: 19-204.
- Janetschek, H. (1990): Als Zoologe am Dach der Welt. – Ber. Nat.-Med. Ver. Innsbruck, Suppl. 6: 119p.
- Jeannel, R. (1950): Hautes montagnes d'Afrique. – Mus. Nat. Hist. Nat. Paris (Suppl.) 1: 1-253.
- Jocqué, R. (1981): Some Linyphiids from Kenya with the description of *Locketidium* n. gen. (Araneida, Linyphiidae). – Rev. Zool. afr. 95(3): 598-569.

- Kauri, H. (1985): Opiliones from Central Africa. – Ann. Mus. R. de l'Afrique Centrale, Tervuren 245 – Sci. Zool.: VIII+168 p.
- Killick, D.J.B. (1978): The Afromontane. – biogeography and ecology of Southern Africa. (ed. Werger, M.J.A.). – Monogr. Biol. 31: 515-560.
- Lange, H. (1985): Kilimanjaro. The white roof of Africa. – Leipzig, 175 pp.
- Lawrence, R.E. (1962): Mission zoologique de l'I.R.S.A.C. en Afrique orientale (P. Basilevsky et N. Leleup, 1957). LXXIV. – Opiliones. – Ann. Mus. Roy. Afr. Centr., 8, Zool. 110: 9-89.
- Lépiney, J. de (1939): Solifuges et Opilionides du Maroc déterminés par le Dr. C.-Fr. Roewer. – Bull. Soc. Sci. nat. Maroc 19: 116-117.
- Lessert, R. de. (1915-1926): Araignées du Kilimanjaro et du Mérou. – Rev. suisse Zool. 23, 27, 28, 31, 33.
- Mahnert, V. (1981): Die Pseudoskorpione (Arachnida) Kenyas I. Neobisiidae und Ideoroncidae. – Rev. suisse Zool. 88(2): 535-559.
- Mahnert, V. (1982a): Die Pseudoskorpione (Arachnida) Kenyas, IV. Garypidae. – Ann. Hist., Nat. Mus. Nat. Hungarici 74: 307-329.
- Mahnert, V. (1982b): Die Pseudoskorpione (Arachnida) Kenyas V. Chernetidae. – Rev. suisse Zool. 89(3): 691-712.
- Mahnert, V. (1983): Die Pseudoskorpione Kenyas VI. Dithidae (Arachnida). – Rev. Zool. afr. 97(1): 141-157.
- Mahnert, V. (1985): Die Pseudoskorpione (Arachnida) Kenyas. VIII. Chthoniidae. – Rev. suisse Zool. 92(4): 823-843.
- Mahnert, V. (1988): Die Pseudoskorpione (Arachnida) Kenyas. Familien Withiidae und Cheliferidae. – Trop. Zool. 1: 39-89.
- Mahunka, S. (1982a): Äthiopische Tarsonemiden (Acari: Tarsonemida), I. – Acta Zool. Acad. Sci. Hung. 21 (3-4): 369-410.
- Mahunka, S. (1982b): Oribatids from the eastern part of the Ethiopian region. I. – Acta Zool. Acad. Sci. Hung. 28 (3-4): 293-336.
- Mahunka, S. (1983a): Oribatids from the eastern part of the Ethiopian region. II. – Acta Zool. Acad. Sci. Hung. 29 (1-3): 151-180.
- Mahunka, S. (1983b): Oribatids from the eastern part of the Ethiopian region (Acari). III. – Acta Zool. Acad. Sci. Hung. 29 (4): 397-440.
- Mahunka, S. (1984a): Oribatids of the eastern part of the Ethiopian region (Acari). V. – Acta Zool. Hung. 30 (1-2): 87-136.
- Mahunka, S. (1984b): Oribatids of the eastern part of the Ethiopian region (Acari) VI. – Acta Zool. Hung. 30 (3-4): 393-444.
- Mani, M.S. (1968): Ecology and biogeography of high altitude insects. – Dr. W. Junk Publ., The Hague, Ser. Entomologica 4: 527 p.
- Martens, J. (1993): Bodenlebende Arthropoda im zentralen Himalaya: Bestandsaufnahme, Wege zur Vielfalt und ökologische Nischen. – In: Neue Forschungen im Himalaya (ed. Schweinfurth, U.). – Erdkundl. Wiss. 112: 231-250.

- Mauriès, J.P., & A. Heymer (1996): Nouveaux micropolydesmides d'Afrique centrale: essai de rassemblement pour une révision du genre *Sphaeroparia* (Diplopoda, Polydesmida, Fuhrmannodesmidae). – Bull. Mus. nat. Hist. nat. Paris, 4e ser. 18, Sect. A (1-2): 165-184.
- Monod, Th. (1957): Les grandes divisions chorologiques de l'Afrique. – C.S.A., Publ. 24, Londres, 147 p.
- Moreau, R.E. (1963): Vicissitudes of the African biomes in the late Pleistocene. – Proc. Zool. Soc. London 141: 395-421.
- Neumann, L.G. (1910): Ixodidae. – In: Wissenschaftliche Ergebnisse der Kilimanjaro-Meru Expedition. (ed. Sjöstedt, Y.) 3: 17-30.
- Nobili, G. (1906): Spedizione al Ruwenzori di S. A. R. Luigi Amedeo di Savoia Duca degli Abruzzi, IX. Crostacei. – Boll. Mus. Zool. Anat. Torino 21(544): 1-2.
- Paulian de Félice, L. (1941): Oniscoides de la côte occidentale d'Afrique III. Eubelidae. – Bull. Soc. Zool. France 66: 50-59.
- Paulian de Félice, L. (1945a): Isopodes. – In: Mission scientifique de l'Omo, VI, 57. Faune des terriers des Rats-taupes. – Mém. mus. nat. Hist. nat. Paris, N. S. 19(1): 311-313.
- Paulian de Félice, L. (1945b): Isopodes terrestres. – In: Mission scientifique de l'Omo, VI, 60 (Zool.). – Mém. mus. nat. Hist. nat. Paris, N.S. 19(2): 331-344.
- Polis, G.A. (1990): Ecology. – pp. 247-293 in: The biology of scorpions (ed. Polis, G.A.). – Stanford Univ. Press, Stanford.
- Reddell, J.R. & J.C. Cokendolpher (1995): Catalogue, bibliography and generic revision of the order Schizomida (Arachnida). – Texas Mem. Mus., Speleol. Monogr. 4: 1-170.
- Ribaut, H. (1914a): Myriapodes. I. Chilopodes. – In: Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912), Résultats scientifique: 1-35.
- Ribaut, H. (1914b): Myriapodes. II. Symphyla. – In: Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912), Résultats scientifique: 39-48.
- Roewer, C.F. (1913): Arachnides I. Opiliones. – In: Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale (1911-1912), Résultats scientifique 1: 1-22.
- Roewer, C.F. (1941): Expedition to South-West Arabia 1937-8. Vol. I, Nos 1-8. Arachnida: Opiliones. – Brit. Mus. (Nat. Hist.): 51-52.
- Roewer, C.F. (1952): Opilioniden und Solifugen aus Ost-Afrika. – Veröff. Mus. Nat.kde. Bremen 2: 87-90.
- Roewer, C.F. (1956): Journey to Northern Ethiopia (Simien), 1952-3: Arachnida, Opiliones. – J. Linn. Soc. Zool., London 43: 93-95.
- Russel-Smith, A. & R. Jocqué (1986): New species and records of Linyphiidae (Araneae) from Kenya. – Rev. Zool. afr. 99: 439-453.
- Salt, G. (1954): A contribution to the ecology of Upper Kilimanjaro. – J. Ecol. 42: 375-423.

- Scharff, N. (1992): The linyphiid fauna of Eastern Africa (Araneae: Linyphiidae) – distribution patterns, diversity and endemism. – Biol. J. Linn. Soc. 45: 117-154.
- Scheller, U. (1954): Symphyla from the Swedish East Africa expeditions in 1937-1938 and 1948, with a summary of the known African species. – Ark. Zool. 7(13): 227-240.
- Schmölzer, K. (1974): Landisopoden aus Zentral- und Ostafrika (Isopoda, Oniscoidea). – Sitzungsber. Österr. Akad. Wiss., Mathem.-naturw. Kl., 1, 182(1-5): 147-200.
- Scott, H. (1958): Biogeographical research in High Simien (northern Ethiopia), 1952-53. – Proc. Linn. Soc., London 170(1): 1-85.
- Silvestri, F. (1907): Spedizione al Ruwenzori di S.A.R. Luigi Amedeo di Savoia, duca degli Abruzzi. XXVI. Nuova specie de simfili *Scutigereella ruwenzorii*. – Boll. Mus. Zool. Anat. comp. Univ. Torino 22.
- Sjöstedt, Y. (1910): Wissenschaftliche Ergebnisse der schwedischen zoologischen Expedition nach dem Kilimanjaro, dem Meru und den umgebenen Massaistuppen Deutsch-Ostafrikas 1905–1906. – Stockholm, 3 vols.
- Sörensen, W. (1910): Arachnoidea. Opiliones. In: Wissenschaftliche Ergebnisse der Kilimanjaro – Meru Expedition (ed. Sjöstedt, Y.). Stockholm, 3: 59-82.
- Starega, W. (1984): Revision der Phalangiidae (Opiliones), III. Die afrikanischen Gattungen der Phalangiinae, nebst Katalog aller afrikanischen Arten der Familie. – Ann. Zool., Warszawa, 38 (1): 1-79.
- Swan, L.W. (1968): Alpine and aeolian regions of the world. – In: Arctic and Alpine environments (ed. Wright, H.E. Jr. & W.H. Osborn).– Indiana Univ. Press, Bloomington: 29-54.
- Taiti, S. & F. Ferrara (1980): The family Philosciidae (Crustacea: Oniscoidea) in Africa, south of the Sahara. – Mon. zool. ital., N.S., Suppl. 4: 53-98.
- Taiti, S. & F. Ferrara (1987): Contributions to the knowledge of the montain fauna of Malawi 6. Terrestrial isopods (Crustacea). – Rev. Zool. Afr. 101 (1): 69-102.
- Trägårdh, I. (1910): Acari. – In: Wissenschaftliche Ergebnisse der Kilimandjaro-Meru Expedition (ed. Sjöstedt, Y.). Stockholm, 3: 31-57.
- Troll, C. (1959): Die tropischen Gebirge. Ihre dreidimensionale klimatische und pflanzengeographische Zonierung. – Bonner Geogr. Abh. 25: 93 p.
- Troll, C. (1961): Klima und Pflanzenkleid der Erde in dreidimensionaler Sicht. – Naturwiss. 48(9): 332-348.
- Troll, C. (1975): Vergleichende Geographie der Hochgebirge der Erde in landschaftsökologischer Sicht. – Geogr. Rundsch. 5: 185-198.
- Tullgren, A. (1910): Araneae. – In: Wissenschaftliche Ergebnisse der Kilimandjaro-Meru Expedition (ed. Sjöstedt, Y.). Stockholm, 3: 85-172.
- Vachon, M. (1945): Mission scientifique de l'Omo, VI. 57. Faune des terriers des rats-taupes. X. Chernètes. – Mém. Mus. Nat. Hist. Nat., N.S. 19(1): 188-197.

- Van Steenis, C. G. G. J. (1935): On the origin of Malaysian mountain flora II. Altitudinal zones, general considerations and renewed statement of the problem. – Bull. Jard. Bot. Buitenzorg, ser. 3, 13(3).
- Verhoeff, K. W. (1937): Über einige *Porcellio*-Arten aus Marokko, gesammelt von Herrn J. de Lépiney. – Zool. Anz. 119: 302 - 307.
- Verhoeff, K. W. (1938a): Über Land-Isopoden aus Marokko. II. Teil. – Zool. Anz. 124: 61-67.
- Verhoeff, K. W. (1938b): Myriapoden aus Marokko. II. Teil (Gesammelt von Herrn J. de Lépiney). – Zool. Anz. 123: 295-302.
- Wesolowska, W. (1986): A revision of the genus *Heliophanus* C.L.Koch, 1833 (Aranei: Salticidae). – Ann. Zool., Warszawa, 40(1): 1-254.
- White, F. (1978): The Afromontane region. – pp. 463-513 in: Biogeography and ecology of southern Africa (ed. Werger, M.J.A.) – Mon. Biol. 31, Dr W. Junk Publ., The Hague.
- Zacharda, M. & M. Daniel (1987): The first record of the family Rhagidiidae (Acarina: Prostigmata) from the Himalayan region. – Vest. (s. Spole). zool. 51: 58-59.

Appendix

Isopoda, Arachnida and Myriapoda known to live in the Afrotropical oréal above 3500 m (in brackets the main authors for those groups)

Isopoda (Barnard 1940, Budde-Lund 1910, Paulian de Félice 1941, 1945a,b, Ferrara & Taiti 1984, Taiti & Ferrara 1980, Nobili 1906, Scott 1958, Schmölzer 1974)

Fam. Eubelidae

Aethiopopactes chenzemae Ferrara et Taiti - 4600 m, Kilimanjaro

Benechinus armatus Budde-Lund - 4600 m, Mt Meru

Mesarmadillo chappuisi Paulian de Félice - 4000 m, Mt Elgon

M. arambourgi Paulian de Félice - 4000 m Mt Elgon

Hiallelgon jeanneli Paulian de Félice - 4000 m on Mt Elgon

"*Periscyphis*" *montanus* Schmölzer - 3800 m, Mt Kenya

Hiallum richardsoni Paulian de Félice - 3500 m, Mt Elgon

Periscyphis ruficauda Budde-Lund - 3500 m, Mt Kenya

Eubelum tachyorictidis Paulian de Félice - 3500 m, Mt Elgon

Microcercus sp. - 3455 m, Ethiopia

Fam. Philosciidae

Afrophiloscia uncinata Ferrara - 3700 m, Kilimanjaro

Fam. Porcellionidae

"*Porcellio*" *spatulata* Barnard - 3600 m, Ethiopia

Fam. Armadillidae

"*Synarmadillo*" *marmoratus* Budde-Lund - 3500 m, Mt Meru

Arachnida

Scorpionida (Tullgren 1910)

Fam. Buthidae

Uroplectes fischeri Tullgren - 3500 m, Mt Meru

Pseudoscorpionida (Beier 1944, 1951, 1955, 1959, 1962, Vachon 1945, Mahnert 1982a,b, 1983, 1985, 1988)

Fam. Olpiidae

Calocheiridius crassifemoratus Beier - 3650 m, Mt Elgon

Fam. Atemnidae

Titanatemnus palmquisti (Tullgren) - 4100 m, Kilimanjaro

Fam. Chernetidae

Nudochernes crassus Beier - 3700 m, Mt Elgon

N. montanus Beier - 3500 m, Mt Elgon

N. robustus Beier - 3500 m, Mt Elgon

Fam. Withiidae

Withius somalicus Beier - 3500 m, Mt Elgon

Opiliones (Sörensen 1910, Goodnight & Goodnight 1959, Roewer 1913, 1941, 1952, 1956, Lawrence 1962, Kauri 1985)

Laniatores

Fam. Assamiidae

Metaereca abnormis Roewer - 4000 m, Ruwenzori

Hypoxestus accentuatus Sör. - 4600 m, Kilimanjaro

H. holmi Goodnight et Goodnight - 4200 m, East Africa

Hypoxestus mesoleucus Sör. - 3500 m, Kilimanjaro

H. patellaris Sör. - 4000 m, Ruwenzori

Ereca undulata Sör. - 4025 m, Kilimanjaro
E. simulator Sör. - 4000 m, Kilimanjaro
E. maculata Roewer - 3975 m, Kilimanjaro
E. lata Sör. - 3500 m, Kilimanjaro
E. affinis Sör. - 3500 m, Kilimanjaro
E. modesta Sör. - 3500 m, Kilimanjaro
Randilea scabricula Roewer - 3630 m, Mt Elgon
Simienatus scotti Roewer - 3505 m, Semien, Ethiopia

Fam. Biantidae

Metabiantes punctatus Sör. - 4000 m, Kilimanjaro
M. trifasciatus Roewer - 3600 m, Mt Meru
M. convexus Roewer - 3500 m, Ruwenzori

Palpatores

Fam. Phalangiidae

Odontobunus africanus Roewer - 3770 m, Kilimanjaro
O. armatus (Sör.) - 4000 m, Kilimanjaro
Rhampsinitus bettoni Pocock - 4600 m, Kilimanjaro
Rh. discolor Karsch - 3870 m, Ruwenzori
Rh. salti Roewer - 3800 m, Kilimanjaro
Rh. soerensemi Starega (= *Rh. pictus* Sör.) - 3500 m, Mt Meru
Rh. (?) mesomelas Sör. - 4000 m, Kilimanjaro
Dacnopilio scopulatus Lawrence - 3600 m, Mt Meru
Gurua africana Karsch - 4000 m, Kilimanjaro
G. frigesceus Loman - 4000 m, East Africa
Cristina pachylomera Simon - 3870 m, Ruwenzori; 3658 m, Semien

Araneida (Benoit 1978, Berland 1914, 1920, Bosmans 1977, 1978, 1979, 1981a,b, Bosmans & Jocqué 1983, Denis 1950, 1962, Fage 1940, Holm 1962, Jocqué 1981, Lessert 1915-1926, Russel-Smith & Jocqué 1986, Scharff 1992, Tullgren 1910, Wesolowska 1986)

Fam. Zodariidae

Mallinella vittiventris Strand - 3500 m, Karisimbi

Fam. Linyphiidae

Araeoncus picturatus Holm - 4650 m, Kilimanjaro
A. subniger Holm - 4400 m, Mt Kenya
A. impolitus Holm - 3900 m, Aberdare
Asthenargus expallidus Holm - 3550 m, Aberdare
A. inermis Simon et Fage - 3480 m, Mt Kenya
A. marginatus Holm - 3450 m, Ruwenzori
Callitrichia ruwenzoriensis Holm - 4930 m, Ruwenzori
C. kenya Fage - 4530 m, Mt Kenya
C. glabriceps Holm - 4200 m, Mt Elgon
C. aliena Holm - 4150 m, Mt Elgon
C. paludicola Holm - 3975 m, Kilimanjaro
C. hamifer Holm - 3800 m, Mt Elgon
C. monticola Tullgren - 3500 m, Kilimanjaro
Ceratinopsis fako Bosmans et Jocqué - 4000 m, Fako, Cameroon
Erigone aethiopica Tullgren - 4200 m, Mt Kenya; 4000 m (Cameroon)
Lepthyphantes kilimanjaricus Tullgren - 4000 m, Kilimanjaro
L. ruwenzori Jocqué - 3800 m, Ruwenzori
Meioneta obscura Denis - 4723 m, Ruwenzori
Microcyba erecta Holm - 4300 m, Ruwenzori
M. hamata Holm - 4300 Mt Elgon
M. annulata Holm - 4000 m, Mt Elgon
Microcyba brevidentata Holm - 3900 m, Kilimanjaro
M. projecta Holm - 3800 m, Ruwenzori
M. hedbergi Holm - 3730 m, Muhavura
M. falcata Holm - 3450 m, Ruwenzori

Nerienne kibonotensis Tullgren - 3500 m, Kilimanjaro
Oreocyba propinqua Holm - 4300 m, Mt Elgon
O. elgonensis Fage - 4200 m, Mt Elgon
Pelecopsis ruwenzoriensis Holm - 4930 m, Ruwenzori
P. biceps Holm - 4300 m, Kilimanjaro
P. alticola Berland - 4165 m, Mt Elgon; 3850 m, Mt Kenya; 3400 m, Aberdara
P. tenuipalpis Holm - 4000 m, Ruwenzori
P. infusca Holm - 4000 m, Ruwenzori
P. senecicola Holm - 3930 m, Ruwenzori
P. pasteurii Berland - 3800 m, Kilimanjaro
P. reclinata Holm - 3760 m, Mt Elgon
P. varians Holm - 3450 m, Mt Elgon
P. flava Holm - 3450 m, Ruwenzori
Toschia telekii Holm - 4300 m, Mt Kenya
T. aberdarensis Holm - 3750 m, Aberdare
Tybaertiella kruegeri Simon - 3750 m, Karisimbi
Walckenaeria meruensis Tullgren - 3820 m, Kilimanjaro; 3280 m, Mt Meru
W. aberdarensis Holm - 3550 m, Aberdare, Mt Kenya
W. ruwenzorensis Holm - 3450 m, Ruwenzori

Fam. Hahniidae

Hahnia tabulicola Simon - 3900 m, Cameroon
H. major Benoit - 3750 m, Mt Kenya
H. sirimoni Benoit - 3750 m, Mt Kenya

Fam. Lycosidae

Pardosa alticola Alderweiltdt et Jocqué - 3700 m, Rwanda; 3650 m, Semien

Fam. Salticidae

Heliophanes crudeni Lessert - 4650 m, Kilimanjaro
H. gladiator Wesolowska - 4450 m, Mt. Kenya
H. imperator Wesolowska - 4200 m, Mt Kenya
H. kenyaensis Wesolowska - 3650 m, Mt Elgon

Acariformes (André 1936, 1938, 1945, 1957, 1965, Balogh 1966, Evans 1953, Mahunka 1982a, b, 1983a, b, 1984a, b, Trägårdh 1910)

Acaridida

Fam. Glycyphagidae

Glycyphagus domesticus (De Geer) - 3500 m, Mt Elgon

Fam. Anoetidae

Histiostoma telatum Mahunka - 3450 m, Kilimanjaro

Prostigmata

Fam. Bdellidae

Bdella piggotti Evans - 3810 m, Kilimanjaro

Fam. Anystidae

Anystis baccharum L. - 3810 m, Kilimanjaro

Fam. Erythraeidae

Charletonia areolata Trägårdh - 3810 m, Kilimanjaro

Fam. Trombidiidae

Trombidium bipectinatum Trägårdh - 3800 m, Mt Meru
T. tinctorium L. - 3800 m, Mt Meru
Trombidium meruense Trägårdh - 3800 m, Mt Meru
T. simile Trägårdh - 3800 m, Mt Meru
Dinothrombium trispilum Berlese - 4200 m, Ruwenzori
D. tarsale Berlese - 4000 m, Mt Elgon
Allothrombium pergrande Berlese - 4000 m, Kilimanjaro

Fam. Microtrombidiidae

Enemothrombium bipapillatum Berlese - 3500 m, Mt Elgon

E. carduigerum Berlese - 3500 m, Mt Elgon

E. jeanneli André - 3500 m, Mt Elgon

Oribatida

Fam. Brachychthoniidae

Liochthonius tanzanicus Mahunka - 3890 m, Kilimanjaro

Fam. Haplozetidae

Protoribates shiraensis Evans - 4590 m, Kilimanjaro

Fam. Euphthiracaridae

Rhysotritia ardua (C.L. Koch) - 3800 m, Kilimanjaro

Fam. Microtegeidae

Microtegeus undulatus Berlese - 4285 m, Kilimanjaro

Fam. Ceratozetidae

Africoribates ornatus Evans - 4590 m, Kilimanjaro

Ghilarovizetes africanus Mahunka - 3900 m, Kilimanjaro

Fam. Tectocepheidae

Tectocephus spinosus Mahunka - 3890 m, Kilimanjaro

Fam. Scutoverticidae

Scutovertex africanus Evans - 4438 m, Kilimanjaro

Fam. Dampfiellidae

Dampfiella setosa Mahunka - 3890 m, Kilimanjaro

Fam. Oppiidae

Oppia nasalis Evans - 4285 m, Kilimanjaro

O. africanus Evans - 4285 m, Kilimanjaro

Amerioppia foveolata Mahunka - 3820 m, Kilimanjaro

Fam. Quadropiidae

Quadropia crenata Mahunka - 3820 m, Kilimanjaro

Fam. Oribatulidae

? *Incabates longisacculus* Mahunka - 3820 m, Kilimanjaro

Nannerlia elongatissima Mahunka - 3890 m, Kilimanjaro

Zygoribatula setosa (Evans) - 3810 m, Kilimanjaro

Fam. Scheloribatidae

Scheloribates laevigatus C.L. Koch - ? 4590 m, Kilimanjaro

Fam. Oribatidae

Oribates geniculatus (L.) - 3810 m, Kilimanjaro

Parasitiformes (André 1938, Neumann 1910)

Gamasida

Fam. Macrochelidae

Macrocheles elgonensis André - 3500 m, Mt Elgon

Fam. Hypoaspidae

Hypoaspis praesternalis Willmann - Kilimanjaro

Ixodida

Fam. Ixodidae

Ixodes ugandanus djaronensis Neumann - 3500 m, Mt Meru

I. rarus Neumann - 3500 m, Mt Meru

Rhipicephalus simus C.L.Koch - 3500 m, Mt Meru

Symphyla (Ribaut 1914b, Silvestri 1907, Scheller 1954)

Fam. Scutigerellidae

Hanseniella ruwenzorii Silvestri - 4500 m, Ruwenzori, 3650 m, Mt Kenya

H. pillipes Attems - 4200 m, Ruwenzori, 4000 m, Mt Elgon

H. afromontana Scheller - 4000 m, Ruwenzori

H. producta Ribaut - 3650 m, Mt Kenya

Chilopoda (Attems 1937, 1939, Ribaut 1914a)

Geophilomorpha

Fam. Mecistocephalidae

Mecistocephalus insularis Lucas - 3900 m, Nyiragongo

M. (sub "*Lamnonyx*") *punctifrons* Newprt - 3500 m, Mt Elgon

Lithobiomorpha

Fam. Henicopidae

Lamyctes africana Poc. - 4200 m, Ruwenzori

L. fulvicornis Meinert - 4000 m, Mt Kenya

Scolopendromorpha

Fam. Scolopendridae

Scolopendra afra Mein. - 4000 m, Mt Elgon

Fam. Cryptopidae

Cryptops numidicus tropicus Attems - 3500 m, Mt Meru

C. incerta Attems - 3500 m, Mt Elgon

C. bottegoi kenyae Rib. - 3500 m, Elgon

Lamnonyx punctifrons Newport - 3500 m, Mt Elgon

Diplopoda (Attems 1909, 1939, Brölemann 1920, Mauriès & Heymer 1996)

Stemmiulida

Fam. Stemmiulidae

Stemmiulus sjostedti Attems - 3500 m, Mt Meru

Polydesmida

Fam. Fuhrmannodesmidae

Elgonicola jeanneli Attems - 3500 m, Mt Elgon

E. jeanneli microchaeta Attems - 4000 m, Mt Elgon

Sphaeroparia petarberoni Mauriès et Heymer - 4200 m, Ruwenzori

S. minuta Attems - 3500 m, Mt Meru

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Two sympatric *Lygodactylus* species in coastal areas of Eastern Africa (Reptilia, Gekkonidae)

Beate Röhl

Abstract: The genus *Lygodactylus* (Reptilia, Gekkonidae) comprises about sixty species of relatively small, diurnal geckos living mainly in Africa and Madagascar. A large group within the genus is the '*Lygodactylus picturatus*' complex whose taxa are either described as subspecies or are treated as individual species depending on authors. Two taxa of this complex occur sympatrically without interbreeding on the coast of Kenya between Mombasa and the Tanzanian border. Whereas these taxa differ only slightly in size and other morphological features like scalation pattern, there are definite differences in the colour patterns and other biological features. *L. picturatus* is characterized by a distinct sexual dichromatism and strong physiological and ontogenetic colour change; in contrast, *L. mombasicus* has only slight sexual dichromatism, only weak physiological and no ontogenetic colour change. The somewhat complicated nomenclature of the species concerned is also discussed.

Key words: East Africa, Reptilia, Gekkonidae, *Lygodactylus*, sympatric species

Introduction

Geckos are typically small, agile lizards, and they are found in tropical and subtropical regions of all continents. Most geckos are nocturnal. However, members of 14 out of approximately 90 genera are diurnal, and between the categories 'nocturnal' and 'diurnal' there are several transitions. Ophthalmological evidence indicates that diurnal geckos have re-acquired diurnal habits from nocturnal gekkonid ancestors (Walls 1942, Röhl 1996). Diurnal geckos are restricted to New Zealand, Central and South America, and Africa, the Middle East and the Indian Ocean Islands. One strictly diurnal genus is *Lygodactylus*, which comprises numerous species of relatively small geckos living in Africa (from about 15° N to 30° S) and Madagascar.

A large and difficult group within the genus is the '*Lygodactylus picturatus*' complex, with many taxa in West, Central and East Africa. Depending on authors, these taxa are either described as subspecies of *L. picturatus* (e.g. Loveridge 1947) or are treated as individual species (e.g. Pasteur 1965).

Many of these taxa are indeed conspecific, despite recognizable differences in size and colour patterns. In Kenya, animals from the coast (*L. p. picturatus*) are able to produce viable offspring with animals from, e.g. Mtito Andei (about 250 km northwest of Mombasa) and from Olorgesailie (in the Rift Valley, about 60 km southwest of Nairobi) (Röhl 1994 and unpubl. observ.). Thus these populations have to be treated as subspecies. As animals from Olorgesailie come close to *L. p. keniensis* Parker, 1936 they are parts of a cline, which may well extend at least to 'typical' *L. p. keniensis* from the northern Rift Valley or even beyond.

On the other hand, there are two *Lygodactylus* taxa on the Kenyan coast that are easily distinguished phenologically and that occur sympatrically, even sharing one tree. They do apparently not interbreed, at least there are no intermediates.

This paper deals with the ecology of these two taxa and with some nomenclatorial problems around them.

Materials and methods

Field observations

Geckos of the genus *Lygodactylus* were studied in February 1992 and March 1997 in Kenya, from the Rift Valley (Lake Bogoria) to the coast. The two taxa concerned were observed primarily in Tiwi Beaches on the coast between Mombasa and the Tanzanian border (4°13'S, 39°36'E). Animals were observed with binoculars for several days. They were common on trees (e.g. coconut palms, but more often other trees, notably those with several trunks) and on walls of buildings.

Breeding

Geckos were kept and bred under laboratory conditions for several years. They were housed in glass terraria containing a layer of sand and various plants, branches, and pieces of bark as hiding places. A 12-hour light/dark cycle was maintained. The temperature varied from 28 to 34 °C during the day and from 23 to 25 °C during the night. The geckos were fed a variety of insects and pieces of banana or mashed fruit. Drinking water was enriched with mineral preparations and vitamins. Eggs were incubated either in the terraria or in a special incubating chamber with thermostat, and the young were reared individually in smaller cages.

Morphological characters

Specimens preserved in 70 % ethanol were investigated from different localities on the East African coast (Kenya: Kikambala, Tiwi Beaches, Diani Beach; Tanzanian coast). For comparison with results by Loveridge (1947), the same morphological characters, i.e. scalation of upper and lower jaw, number of preanal pores, number of pairs of adhesive lamellae and, additionally, number of pairs of adhesive lamellae under the tail tip, were examined. These characters were also checked in living animals.

Results

For description of the two taxa of *Lygodactylus* treated here, the terms *L. p. picturatus* and *L. 'p.' mombasicus* are used *sensu* Loveridge (1947).

Colour patterns

L. p. picturatus is characterized by a distinct sexual dichromatism, which in this taxon attains its greatest development within the genus (Loveridge 1947). Head, neck and shoulders of the territorial male are bright mustard yellow with dark spots or broken streaks (plate 4: a,c, page 192). Back, limbs and tail are bluish-grey, sometimes with light eyespots. Pale lateral stripes extend from the shoulders to the

base of the tail. Breast and belly are white and yellowish orange respectively. The throat is uniformly black (plate 4: d). Males are capable of changing coloration very rapidly, e.g. after disturbance. Within seconds they can become very dark, almost black, without any trace of yellow. Only males have preanal pores.

Head and shoulders of the 'well-poised' female are light yellow with darker spots or streaks (plate 4: b). Back, limbs and tail are light brown to beige-grey with pale lateral stripes extending from the shoulder to the beginning of the tail. Breast and belly are white and whitish yellow respectively. The throat is either uniformly white or marked with a more-or-less faint, mottled greyish chevron-shaped pattern (plate 4: e). Similar to the male, this coloration can change to brown or dull grey. In both sexes this physiological colour change is confined to the dorsal side of the animals.

Hatchlings have a colour pattern similar to that of females but with the head brownish grey, not yellow (plate 4: f). They are able to change their general colour from brownish grey to dark brown. Male offspring develop the typical coloration at an age of about 6 to 8 months.

In contrast, *L. 'p.' mombasicus* has no sexual dichromatism (apart from the colour pattern of the throat) (fig. 1a,b). Both males and females are characterized by a whitish or cream head and neck with clear-cut black markings: black lateral streaks from tip of the nose through the eyes to the shoulders, between the eyes a marking resembling a crown or the letter 'W', on the occiput two fused blotches, on the neck two fused spots which unite with the lateral streak, and above the forelimbs another pair of spots extending posteriorly (fig. 1c). Breast and belly are white and yellow respectively. The sexes can be distinguished by the preanal pores occurring only in males and by the colouring of the throat. The throat of males is almost uniformly black (fig. 1d), whereas that of females is white with a dark chevron-shaped marking (fig. 1e). Hatchlings have the same coloration as adults (fig. 1f). Males, females and hatchlings are capable of changing from a brighter coloration to a duller one, but the typical markings on their heads are always clearly recognizable.

In specimens of both taxa preserved in 70% ethanol, the yellow colour of the belly is destroyed probably because of leaching of pigments into the fixative, whereas the yellow of the head is retained.

Morphological characters

The scalation patterns of the head do not differ in the two taxa of *Lygodactylus* described here (data are summarized in table 1). This is in correspondence with results by Loveridge (1947). Additionally, both taxa possess 6 pairs of adhesive lamellae under the fourth toe. Undamaged tail tips of *L. p. picturatus* and *L. 'p.' mombasicus* are provided with 6 to 8 and 7 to 9 pairs of adhesive lamellae (scansors) respectively. The number of the preanal pores in males was found to be 6 to 8 in *L. p. picturatus* and 10 to 11 in *L. 'p.' mombasicus*.

Adult animals of both taxa are of similar size. Generally, males are slightly larger than females. Eggs of both *Lygodactylus* taxa are indistinguishable.

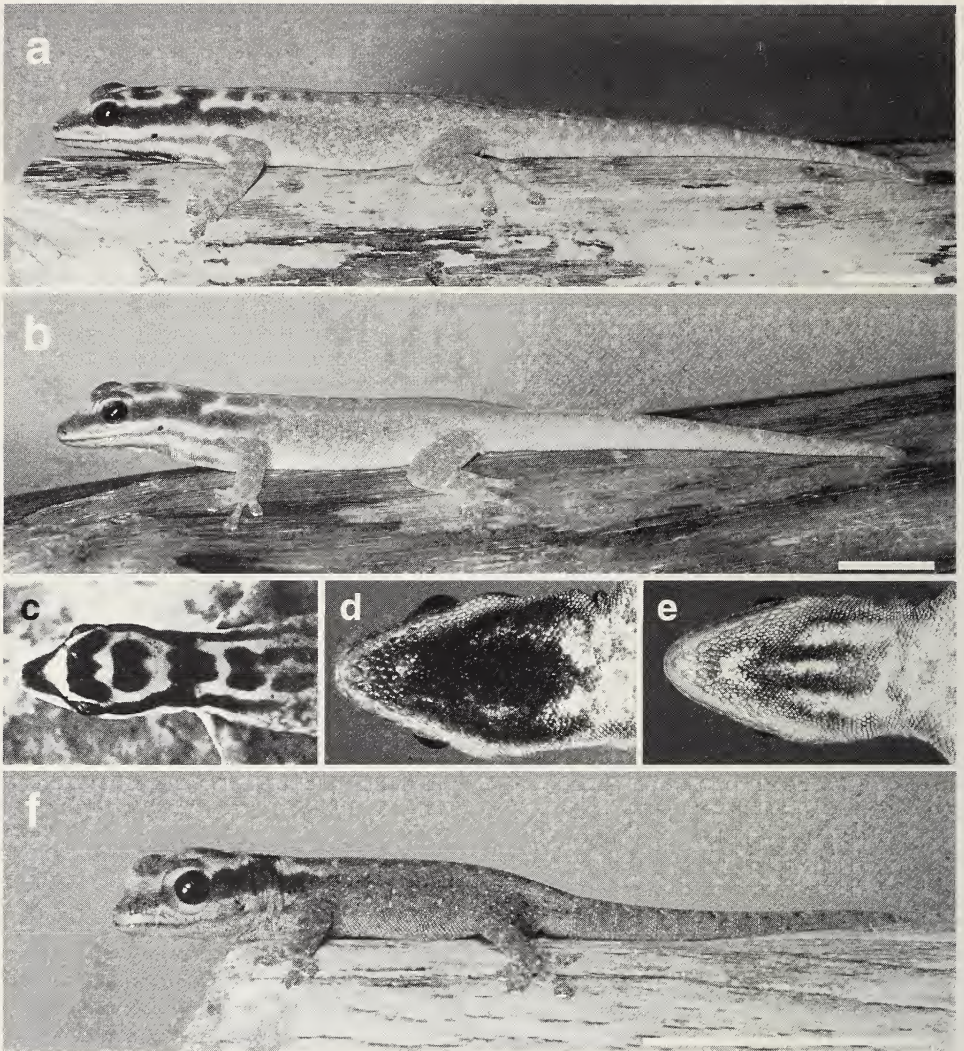


Fig.1: *Lygodactylus* 'p.' *mombasicus* Loveridge, 1935

a) Adult male: head, neck and shoulders with typical black markings, body beige-grey. b) Adult female: colouring as in the male. c) Dorsal view of the head of a female. d) Black throat of a male. e) Throat of a female with a darker chevron-shaped marking. f) Hatchling, two days old: same colour pattern as the adults.

Scale bars 1 cm. All photographs are of live specimens.

Plate 4: *Lygodactylus p. picturatus* (Peters, 1870)

a) Adult male, b) adult female, c) dorsal view of the head of a male. d) Black throat of a male. e) Throat of a female with a faint greyish chevron-shaped marking. f) Hatchling, five days old: juvenile pattern resembling the colour pattern of the female.

Scale bars 1 cm. All photographs are of live specimens.

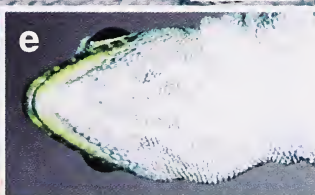
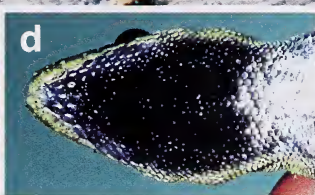


Table 1: Morphological characters of *Lygodactylus p. picturatus* and *L. 'p.' mombasicus*

	<i>Lygodactylus p. picturatus</i>		<i>Lygodactylus 'p.' mombasicus</i>	
	data from Loveridge 1947	own data	data from Loveridge 1947	own data
internasal granules	1-2	1	1-2	2
nasals surrounding nostril	2-3	2-3	2-3	2-3
rostril enters nostril	no	no	no	no
upper labials	6-9	6-7	6-9	7-9
lower labials	5-8	6-7	5-8	5-7
postmentals	3	3	3	3
scansors under fourth toe	5-6	6	5-6	6
scansors under tail tip	no data	7-9	no data	8-9
male (preanal) pores	6-8 (-12)	6-8	6-10	10-11
snout to vent length ♂ (mm)	43	40	39	42
snout to vent length ♀ (mm)	38	36	37	38
snout to vent length of hatchlings	no data	12.5-14	no data	12-14
diameter of eggs (mm)	no data	4.5-6	no data	4.5-6

Field observations

Tiwi Beaches is a ‘standard’ East African coastal area. *L. p. picturatus* inhabits trees on the beach and in gardens, as well as walls of buildings. These geckos live in small groups, usually consisting of one male and one or two females. On palm trees, usually only one pair of *L. p. picturatus* was found. Big trees with several trunks and branches may be inhabited by more than one group. *L. 'p.' mombasicus*, also strictly arboreal and living in groups with one male, was not observed on palm trees and buildings but only on bigger trees on the beach and in gardens. Here, groups of *L. 'p.' mombasicus* and *L. p. picturatus* can coexist on the same tree without apparent interference. The typical intraspecific threat display (curved,

Table 2: Biological characters of *Lygodactylus p. picturatus* and *L. 'p.' mombasicus*.

<i>Lygodactylus p. picturatus</i>	<i>Lygodactylus 'p.' mombasicus</i>
<ul style="list-style-type: none">– ♂: head bright yellow with irregular dark spots or broken streaks; body bluish grey; throat uniformly black– distinct sexual dichromatism: ♀ head yellowish brown with dark spots or streaks; body beige greyish; throat white or weakly marbled– strong physiological colour change– marked ontogenetic colour change, especially in ♂♂	<ul style="list-style-type: none">– ♂: head whitish with characteristic, well-defined dark markings; body beige-grey; throat uniformly black– sexual dichromatism slight (in ♀ throat with dark chevron only)– physiological colour change weak– no ontogenetic colour change
sympatric occurrence of both taxa without interbreeding on Kenyan coast	

arched, laterally flattened body) of *Lygodactylus* males was not observed between males of different taxa.

Only animals with the typical colour pattern of either *L. p. picturatus* or *L. p. mombasicus* were found both at Tiwi Beaches and Diani Beach. There were no intermediates between the two distinct colour patterns.

Discussion

Two taxa of the genus *Lygodactylus* occur sympatrically at the coast between Mombasa and the Tanzanian border. They were treated by Loveridge (1947) as *L. picturatus picturatus* and *L. 'p.' mombasicus*.

Whereas these taxa differ only slightly in their sizes and other morphological features (like scalation pattern), there are definite differences in their colour patterns and other biological features (tables 1+2). *L. p. picturatus* is characterized by a distinct sexual dichromatism and strong physiological and ontogenetic colour change; in contrast, *L. 'p.' mombasicus* has only slight sexual dichromatism, only weak physiological and no ontogenetic colour change.

Both *Lygodactylus* taxa are strictly arboreal and live in small groups, usually consisting of one male with one or a few females. Bigger trees with multiple trunks can be inhabited by several groups of one or both taxa.

While there certainly are olfactory elements, the bulk of the social behaviour of *Lygodactylus* is visually guided. Males of both taxa occupy and patrol territories that are defended by visual threat displays and fights. Aggressive displays are commonly directed towards conspecific males and females. In contrast, there seems to be little or no interference between members of different taxa.

It is remarkable that two *Lygodactylus* taxa with such similar ecological requirements can coexist in the same area, since interspecific competition should be expected. Although it is not uncommon to find both taxa on the same tree, more often each taxon inhabits its own tree. Interspecific competition may be reduced by partly partitioning the habitat, e.g. by inhabiting different vegetation types. *L. p. picturatus* often uses palm trees and buildings where *L. 'p.' mombasicus* was not found. The two taxa meet on multi-stemmed trees where the different trunks could be 'divided' between the taxa. However, it was also observed that both taxa shared a single-stemmed tree.

In the South Turkana region of Kenya, Greer (1967) observed a very similar situation between two *Lygodactylus* species (*L. picturatus keniensis* Parker, 1936 and *L. somalicus battersbyi* Pasteur, 1962). Although being ecologically very similar, these species occur sympatrically in this area, where they inhabit *Acacia* trees. In general, one species occupies one tree, but sometimes both species occur on the same tree, usually a larger one. *L. picturatus keniensis* and *L. somalicus battersbyi* differ conspicuously in their colour patterns, as do *L. p. picturatus* and *L. 'p.' mombasicus*, and Greer also never observed the typical display behaviour interspecifically. In that case, however, there was a clearly dominant taxon: confrontations between the two species resulted in the considerably smaller *L. somalicus battersbyi* being chased away.

Another example is the sympatric occurrence of *L. chobiensis* and *L. capensis* in Zambian woodlands (Simbotwe 1983). These species, too, are ecologically very similar. They reduce competition by partitioning their habitat. The larger *L. chobiensis* was more often found on live trees, whereas *L. capensis* was more commonly found on dead ones. Additionally, *L. chobiensis* occupies on average higher perches than *L. capensis*. This could be confirmed in Popa Falls (Caprivi Strip, Namibia), although it was not unusual there to find both species on the same live tree (Röll 1999).

In contrast to these cases local variants of *L. picturatus* e.g. the populations found in Mtito Andei and Olorgesailie are not separated ecologically. Apparently they are elements of a continuous cline.

Taxonomical and nomenclatorial problems

As *L. p. picturatus* and *L. 'p.' mombasicus* occur sympatrically without interbreeding, and show distinct differences in male/female colouring and in physiological and ontogenetic colour change, they should consequently be treated as distinct species. However, the nomenclature of this group is somewhat complicated. Peters described *L. picturatus* (as *Hemidactylus picturatus*) in 1870. The use of the name *L. picturatus* for the 'yellow-headed' taxon was the common usage during the following hundred years (e.g. Boulenger 1885, Parker 1942, Pasteur 1960, Wermuth 1965, Howell 1981, Welch 1982). In 1935, Loveridge described the 'black-and-white-headed' taxon as subspecies *L. p. mombasicus*.

In a revision of the genus *Lygodactylus*, Pasteur (1965) states that 'to his knowledge' the holotype of *L. picturatus* is a typical *L. 'p.' mombasicus* as defined by Loveridge (1947). Though this statement would upset the widely used nomenclature of the whole group, it is not substantiated further. It remains unclear whether Pasteur actually saw the types; anyway, the otherwise rather vague original description by Peters (1869, *sic*!) states that the male has a yellowish head, and does not mention any bold black markings. This question has to be left open for the time being. Consequently, Pasteur treated *L. picturatus mombasicus* as a synonym of *L. picturatus* and described the 'yellow-headed' dwarf gecko as a new species, *L. luteopicturatus*. However, he did apparently not check whether any of the numerous older names for this taxon were nomenclatorially available (see e.g. the synonymic list in Loveridge 1947). Since then, the name *L. luteopicturatus* has been used by only a few authors for the 'yellow-headed' dwarf gecko (e.g. Pakenham 1983, Broadley & Howell 1991), while the name *L. picturatus* was equally rarely used for the 'black-and-white-headed' dwarf gecko (e.g. Broadley & Howell 1991). In a recent checklist of the geckos of the world, all names for the 'yellow-headed' and the 'black-and-white-headed' dwarf geckos are listed simultaneously (Welch 1994).

So, there are two general lines of argument. If one follows Loveridge's (1947) definitions, the 'yellow-headed' taxon has to be named *L. picturatus*, while the 'black-and-white-headed' taxon is definitely *L. mombasicus*. In this case, Pasteur's *L. luteopicturatus* (1965) is merely a synonym of *L. picturatus*.

If one were to accept Pasteur's (1965) statement about the identity of the holotype of *L. picturatus*, the situation is more complicated. The 'black-and-white-headed' taxon would simply become *L. picturatus*. The 'yellow-headed' taxon, however, has been described several times since Peters's original description of *L. picturatus*. It is rather probable that there are available names for this taxon, e.g. Tornier's (1896) 'variations' (perhaps 'modern' subspecies; cf. Kraus 1973) *griseus*, *septemlineatus* or *quiquelineatus*, Boettger's *quinque-lineata* (1913) or Loveridge's *manni* (1928). If any of these is indeed available, *luteopicturatus* again becomes a synonym.

For these reasons, and to retain stability of a name in common usage, I suggest rejecting Pasteur's questionable proposal until definitely substantiated. This will require examining the type material of the various taxa mentioned in the previous paragraph. This study is currently undertaken. Until then, the widely accepted name *L. picturatus* (Peters, 1870) for the 'yellow-headed' taxon should be retained, as e.g. faunistic appers can suffer substantially from an unclear nomenclatorial situation. Consequently, the 'black-and-white-headed' taxon would have to be treated as *L. mombasicus* Loveridge, 1935, as it has been shown herein to be specifically distinct from *L. picturatus*.

Zusammenfassung

Die Gattung *Lygodactylus* (Reptilia, Gekkonidae) umfaßt ca. 60 Arten relativ kleiner, tagaktiver Geckos, die hauptsächlich in Afrika und Madagaskar leben. Eine große Gruppe innerhalb der Gattung ist der '*Lygodactylus picturatus*'-Komplex, dessen Taxa je nach Autor entweder als Subspecies oder als individuelle Arten beschrieben werden. Zwei Formen dieses Komplexes kommen sympatrisch und reproduktiv isoliert an der Küste Kenias zwischen Mombasa und der Grenze Tanzanias vor. Die beiden Taxa unterscheiden sich nur geringfügig in der Größe wie auch in anderen morphologischen Merkmalen, z.B. in der Beschuppung. Dagegen gibt es deutliche Unterschiede in ihren Farbmustern und anderen biologischen Merkmalen. So ist *L. picturatus* charakterisiert durch auffälligen Geschlechtsdichromatismus und durch ausgeprägten physiologischen sowie ontogenetischen Farbwechsel. Im Gegensatz dazu weist *L. mombasicus* einen nur gering entwickelten Geschlechtsdichromatismus und einen schwach entwickelten physiologischen sowie keinen ontogenetischen Farbwechsel auf. Die Nomenklatur der betreffenden Arten wird diskutiert.

References

- Boettger, O. (1913): Reptilien und Amphibien von Madagaskar, den Inseln und dem Festland Ostafrikas. – pp.269-376, pl. XXIII-XXX in Reise in Ostafrika (ed. Voeltzkow, A.). Vol.3. – Stuttgart
- Boulenger, G.A. (1885): Catalogue of the lizards in the British Museum (Natural History). – London 2nd ed. Vol. 1: 1-497.
- Broadley, D.G. & K.M. Howell (1991): A check list of the reptiles of Tanzania, with synoptic keys. – Syntarsus 1: 1-70.

- Greer, A.E. (1967): The ecology and behavior of two sympatric *Lygodactylus* geckos. – *Breviora* 268: 1-19.
- Howell, K.M. (1981): Notes on two diurnal geckos, *Lygodactylus picturatus* and *Phelsuma dubia*. – *East Afr. Nat. Hist. Soc. Bull.* 3: 43-45.
- Kraus, O. (1973): Internationale Regeln für die Zoologische Nomenklatur: Bericht über Änderungen, gültig ab 1. Januar 1973. – *Senckenbergiana biol.* 54: 219-225.
- Loveridge, A. (1928): Description of a new species of gecko from Tanganyika Territory. – *Proc. U.S. Nat. Mus.* 72 (Art.24): 1-2.
- Loveridge, A. (1935): New geckos of the genus *Lygodactylus* from Somaliland, Sudan, Kenya, and Tanganyika. – *Proc. Biol. Soc. Washington* 48: 195-200.
- Loveridge, A. (1947): Revision of the African lizards of the family Gekkonidae. – *Bull. Mus. Comp. Zool.* 98: 1-469.
- Pakenham, R.H.W. (1983): The reptiles and amphibians of Zanzibar and Pemba Islands (with a note on the freshwater fishes). – *J. East Afr. Nat. Hist. Soc. Nat. Mus.* 177: 1-40.
- Parker, H.W. (1942): The lizards of British Somaliland. – *Bull. Mus. Comp. Zool. Harvard* 91:1-101.
- Pasteur, G. (1960): Notes préliminaires sur les *Lygodactyles* (Gekkonidés). I. Remarques sur les sous-espèces de *Lygodactylus picturatus*. – *Bull. I. F. A. N., Ser. A*, 22: 1441-1452.
- Pasteur, G. (1962): Notes préliminaires sur les lygodactyles (Gekkonidés). II. Diagnose de quelque *Lygodactylus* d'Afrique. – *Bull. I. F. A. N., Ser. A*, 24: 606-614.
- Pasteur, G. (1965): Recherches sur l'évolution des lygodactyles, lézards afro-malgaches actuels. – *Trav. Inst. Scient. Chérif., Sér. Zool.*, 29: 1-132.
- Peters, W. (1869): Mitteilung über eine neue Nagergattung, *Chiropodomys penicillatus*, so wie über einige neue oder weniger bekannte Amphibien und Fische. – *Monatsber. Akad. Wiss. Berlin*: 448-461.
- Peters, W. (1870): Beitrag zur Kenntnis der herpetologischen Fauna von Südafrika. – *Monatsber. Akad. Wiss. Berlin*: 110-115.
- Röll, B. (1994): *Lygodactylus picturatus* (Peters). – *Sauria* 16 (3) Suppl.: 307-310.
- Röll, B. (1999): *Lygodactylus chobiensis* (FitzSimons). – *Sauria* 21(3) Suppl.: 457-460.
- Röll, B., R. Amons & W.W. de Jong (1996): Vitamin A₂ bound cellular retinal-binding protein as ultraviolet filter in the eye of the gecko *Lygodactylus picturatus*. – *J. Biol. Chem.* 271: 10437-10440.
- Simbotwe, M.P. (1983): Comparative ecology of diurnal geckos (*Lygodactylus*) in Kafue flats, Zambia. – *Afr. J. Ecol.* 21: 143-153.
- Tornier, G. (1896): Die Kriechtiere Deutsch-Ost-Afrikas. – Berlin.
- Walls, G. (1942): The vertebrate eye and its adaptive radiation. – Cranbrook Institute of Science, Bloomfield Hills.
- Welch, K.R.G. (1982): Herpetology of Africa: A checklist and bibliography of the orders Amphisbaenia, Sauria and Serpentes. – Robert E. Krieger Publishing Company, Malabar, Florida.

Welch, K.R.G. (1994): Lizards of the world: a checklist. 1. Geckos. – Longdunn Press Ltd, Bristol, England.

Wermuth, H. (1965): Liste der rezenten Amphibien und Reptilien: Gekkonidae, Pygopodidae, Xantusiidae. – Walter de Gruyter & Co., Berlin.

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Comparative ecology and morphology of snipes (family Scolopacidae) in Africa

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Abstract: Six of the 19 existing snipe species occur in Africa, four as Palearctic migrants and two as resident breeding birds. The resident species are the continental African Snipe *Gallinago nigripennis* and Madagascar Snipe *Gallinago macrodactyla* which is endemic to the island of Madagascar. The Palearctic migrant snipes which winter in Africa (i. e. Jack Snipe *Lymnocyptes minimus*, Common Snipe *Gallinago gallinago*, Great Snipe *Gallinago media* and Pintail Snipe *Gallinago stenura*) show some eco-morphological similarities with the African Snipe but all exhibit distinct differences in their social behaviour and life-history patterns from the Madagascar Snipe. In this study we investigated the breeding biology of the African Snipe in the highlands of central Kenya and sought to explain the evolutionary mechanisms that would have produced species segregation, variation in social behaviour and life-history patterns of snipes in Africa.

Key words: Kenya, Africa, *Gallinago nigripennis*, snipes, evolution

Introduction

The ecology and morphology of a species provide special windows for investigating the process of evolution. This is mainly because variations that are produced through evolutionary processes and adaptation to different environments can be inferred or observed from changes in body structure, social behaviour, ecology and life-history patterns (Futyuma 1979).

This study seeks to determine the ecological and morphological adaptations that have permitted the survival and spread of six species of snipes to different environments and geographical regions, especially in Africa. Much of this paper deals with a synthesis of the principles of ecology, morphology and social biology in as much as they assist in the understanding of evolutionary trends in snipes. Our synthesis draws from existing information and from our field studies of the African Snipe in Kenya.

Taxonomy and distribution

Snipes belong to a heterogeneous and cosmopolitan order (Charadriiformes) which contains small waders that inhabit shorelines of lakes and seas, banks of rivers, marshes, cultivated fields and short grasslands. The various species that constitute this diverse group of birds are ecologically isolated through differences in food, habitat and geographical region.

Hayman et al. (1986) recognized 18 species, while Sibley & Monroe (1990) recognized 19 species of snipes occurring in different parts of the world. The continent of Africa has two resident species and four Palearctic migrant species of snipes (Table 1). The Madagascar Snipe (*Gallinago macrodactyla*) is endemic to the island of Madagascar while the African Snipe (*G. nigripennis*) only occurs on the continent.

Table 1: The movement status and distribution of the various species of snipes in Africa

Species	Scientific name	Status	Distribution
Pintail Snipe	<i>Gallinago stenura</i>	Resident/breeding	Somalia and Kenya
African Snipe	<i>Gallinago nigripennis</i>	Migrant/non-breeding	Central, East and S. Africa
Madagascar Snipe	<i>Gallinago macrodactyla</i>	Resident/breeding	Eastern Madagascar
Great Snipe	<i>Gallinago media</i>	Resident/breeding	All Africa
Common Snipe	<i>Gallinago gallinago</i>	Migrant/non-breeding	All Africa
Jack Snipe	<i>Lymnocyrtus minimus</i>	Migrant/non-breeding	East and West Africa

The African Snipe and the Madagascar Snipe exhibit distinct distributions (Urban et al. 1986). The Madagascar Snipe is confined to the island of Madagascar and is therefore geographically isolated from other snipes that occur on the continent. This species exhibits distinct morphological and ecological differences from the continental snipes, reflecting its long period of geographical and genetic isolation.

The African Snipe is resident and breeds in eastern and southern Africa. The species distribution in the continent shows three distinct sub-populations or races. The sub-population *Gallinago nigripennis aequatorialis* (Rueppell) occurs in the region between the Ethiopian highlands and the Democratic Republic of Congo, including East Africa south to Malawi and northern Mozambique. The *Gallinago nigripennis angolensis* (Bocage) sub-population occurs in Angola, Botswana, Namibia, western Zimbabwe, Zambia and south Katanga in Congo. The nominate subspecies *Gallinago n. nigripennis* (Bonaparte) inhabits South Africa and southern Mozambique.

The Palearctic snipes (table 1) occur widely in the continent but mainly within the tropics (Urban et al. 1986). The presence of these snipes in Africa enhances competition with resident snipes for the available food resources but has no significant impact on their reproductive success (Moreau 1972). In our central Kenya study site (Lake Ol Bolossat, 0° 09'S, 36° 09'E) the African Snipe is resident, while the Common Snipe is a regular visitor. The Jack Snipe, Great Snipe and Pintail Snipe occurred there in the 1980s, but over the last 20 years have become extremely rare.

Snipe Populations

The populations of snipes in Africa are not well documented. However, annual African Waterbird censuses, which are co-ordinated by Wetlands International, during the period between 1991 and 1997 indicate low numbers of individuals throughout the continent (table 2). These counts are usually carried out in January and February when Palearctic snipes are in the continent and in June and July when



Fig.1: Distribution of various species of snipes in Africa (source: annual waterbird census 1991-1997).

they have returned to their breeding areas in Europe and northern Asia. The Common Snipe and the African Snipe are abundant in all parts of their range within the continent. The Jack Snipe and Pintail Snipe occur in extremely low numbers. The Great Snipe has also become extremely rare in East Africa during the last 20 years (Zimmerman et al. 1996). The records of snipes often show an aggregated number of birds called *Gallinago* sp., which implies that the various species of snipes are not easy to differentiate in the field during the counts.

Table 2: Total number of various species of snipes recorded in Africa during January and July waterfowl counts between 1991 and 1997.

Snipe species	1991	1992	1993	1994	1995	1996	1997	Total
Jack Snipe	-	11 (1)	2 (1)	-	1 (1)	2 (2)	-	15
Common Snipe	46 (4)	-	71 (3)	80 (2)	1879 (10)	190 (12)	127 (4)	2383
African Snipe	-	51 (4)	104 (5)	24 (3)	404 (7)	276 (10)	227 (4)	1086
Pintail Snipe	2 (1)	-	8 (3)	12 (2)	-	17 (5)	3 (3)	42
Great Snipe	3 (1)	229 (6)	4 (1)	-	82 (4)	25 (4)	83 (7)	426
Madagascar Snipe	-	-	5 (1)	-	-	-	-	5
<i>Gallinago</i> species	-	-	34 (2)	-	351 (3)	9 (3)	86 (3)	478

Note: Numbers in brackets represent the number of African countries that submitted records to Wetlands International

There are better pre-1990 records and counts of snipes in West and South Africa than in East and Central Africa. However, this situation has been changing, with many countries in East and Central Africa starting to count and study snipes. Snipe populations in various African countries are relatively small as indicated by counts made between 1991 and 1997 (see fig.1). The low numbers may be linked to increasing aridity, water pollution, loss of wetlands, and counters insufficient in numbers or experience in the continent. However, the number of countries participating in the annual waterfowl counts in Africa has been gradually increasing and counts are becoming more regular. Data collection is also improving as more researchers study snipes in different parts of the continent.

Morphological characteristics

Body size, including bill size, are important characters influencing the outcome of interspecific and intraspecific competition in birds. Competition between individuals for common resources as well as changes in resource abundance and availability generate adaptations which enable a particular population or sub-population to successfully colonize new habitats and exploit new niches. Differences in body size of various snipe species permit niche separation and hence minimize the negative effects of competition for food. Examination of variations in body measurements of Palearctic and resident snipes in Africa provides insight into the strategies that have enabled those waders to co-exist while utilizing similar habitats. Body size measurements provided in table 3 indicate that the Jack Snipe is the smallest and Madagascar Snipe the largest of the six species examined in this study. In evolutionary terms, Jack Snipe is perhaps the most advanced while Madagascar Snipe may be the most primitive. The African Snipe, Common Snipe, Pintail Snipe and Great Snipe are of intermediate size. Interspecific competition for food resources is likely to be intense among individuals of almost the same body size, especially where they share similar foraging habitats. The four species of snipes forage together in Africa during the boreal winter.

Table 3: Major body measurements of the various snipe species occurring in Africa Males and females combined).

Species	Ranges of body size measurements (mm)			
	Body length	Wing length	Tarsus length	Bill length
Jack Snipe	170-190	105-121	22-25	36-43
Common Snipe	250-270	123-144	27-36	55-75
African Snipe	255-285	128-141	34-41	67-96
Great Snipe	270-290	139-155	32-40	54-72
Pintail Snipe	250-270	125-143	29-36	55-70
Madagascar Snipe	290-320	141-149	40-43	80-115

Snipes are fast-flying birds. Migrant birds fly over long distances while the resident African Snipe makes considerable seasonal movements within its range. In terms of wing length, the Jack Snipe is again the smallest while the Madagascar Snipe is the largest. The other snipes fall in an intermediate wing length category. In terms of tarsus length, the Jack Snipe is the smallest and the Madagascar Snipe the largest, with the other four forming a cluster between the two.

Females tend to be slightly larger than males, especially in bill length. Bill length has a direct relationship with food acquisition and hence competition. In terms of bill length, the Jack Snipe has the smallest with Common Snipe and Great Snipe occupying intermediate sizes. Madagascar Snipe and African Snipes have considerably longer bills than the Palearctic migrant snipes.

Breeding

Habitat

All six species of snipes that occur in Africa, including Madagascar, inhabit and breed in wet areas. The Palearctic species, particularly the Jack Snipe and Great Snipe, breed in the cold areas of northern Europe and Asia. The Common Snipe breeds in warmer environments in Central Europe and Central Asia. The two species that breed in Africa also nest in cold but high altitude areas. The African Snipe breeds in highland bogs at altitudes of 1700-4000 m a.s.l., while the Madagascar Snipe breeds in upland marshes but occupies altitudes ranging from 0

Table 4: Breeding habitats of the various species of snipes occurring in Africa

Jack Snipe	Open boreal marshland
Great Snipe	Moist wooded boreal tundra
Pintail Snipe	Flooded sedge and moist grassland
Common Snipe	Fresh or brackish water, marshland with rich tussock sedges, damp farmland
African Snipe	Wet moorland, highland bogs and swamps
Madagascar Snipe	Sedge swamps, rice fields, small bogs and banks of streams

to 2500m in eastern Madagascar. The Common Snipe breeds in open wetlands with relatively short grass or sedges (table 4). The Jack Snipe breeds in open boreal marshland, while the Great Snipe nests in moist wooded boreal tundra. The breeding habitat of the Great Snipe extends to dry land with scattered clumps of vegetation. The breeding habitat of the Common Snipe is generally similar to that of the African Snipe and Madagascar Snipe. All three species build nests on moist ground with a rich community of tussock grass or sedges.

The natural vegetation in which the nest is built shields the nesting bird and the nest contents from strong wind. It also provides shade for the eggs and brood during hot periods of the day as well as concealment from predators. Except for local differences in the choice of nest sites all the six species of snipes breed in similar habitats and cold environments.

Behaviour

Snipes are cryptically coloured, secretive, partly nocturnal and inhabit marshy areas, all of which make their study extremely difficult. Furthermore, the sexes look alike and young birds are difficult to distinguish from adults. Information on breeding behaviour is therefore scanty for most species. However, available information reveals considerable similarities in reproductive behaviour of the different snipe species that breed in Europe and Africa.

One of the most conspicuous behaviours of breeding snipes is the aerial courtship display, known as drumming. This behaviour comprises circular flights broken by vertical dives from heights of between 60m and 100m (Reddig 1978, Gichuki et al. 1998). Most drumming is carried out by males but the receptive female may also drum early in the breeding season (Perrins & Middleton 1987).

Snipes that occur in Africa show some common features of reproductive behaviour (table 5). Except for the African Snipe, which has a monogamous mating system (Urban et al 1986, Gichuki et al. 1998), the other five species exhibit a polygynous mating system. In the case of the Great Snipe, for instance, small groups of males display together in clearly defined lekking sites which can easily be recognized even after the birds have left (Hayman et al. 1986).

In the Pintail Snipe, males competitively perform aerial displays which are equivalent to the leks of the Great Snipe. Females are attracted to the display areas where successful males mate with more than one female.

Table 5: Common features of reproductive strategies and behaviour of the six snipe species found in Africa

Species	Mating system	Nest site	Clutch size	Parental Care
Jack Snipe	Polygynous	Moist ground	3-4	Female
Common Snipe	Polygynous	Moist ground	3-4	Female
African Snipe	Monogamous	Moist ground	3-4	Biparental
Great Snipe	Polygynous	Moist ground	3-4	Female
Pintail Snipe	Polygynous	Moist ground	3-4	Female
Madagascar Snipe	Polygynous	Moist ground	3-4	Female

Jack Snipe males hold a territory of up to 20 ha and advertise it by performing high aerial displays. A Great Snipe male defends a large territory of up to 100 ha in which it mates with several females and defends them against competitors.

Madagascar Snipe males also defend females. In contrast, Common Snipe and African Snipe males make flight displays solitarily in the breeding area and do not maintain exclusive territories. In fact, African Snipe males make flight displays in the breeding area without any observable aggressive encounters (pers. obs.).

There is little variability in nest site among the various species of snipes which breed in Europe and Africa. In all species nests are placed on moist ground with short grass or sedges. The African Snipe places its nest on raised platforms or on top of a tussock of grass which is about 10-15 cm above ground level (Gichuki et al. 1998). The nests of snipes are likely to be flooded by water if they are placed on lakeshores or seasonally flooded depressions. Water level or depth is therefore a critical factor influencing nest placement and nest success in snipes (Gichuki et al. 1998).

There is also little variability in clutch size, with females of most snipe species laying 3-4 eggs. The pear-shaped eggs are proportionally large, the clutch accounting for 60% of the female's body weight in African Snipe (pers. obs.). Females of the migrant snipes lay one clutch per year but lost clutches are replaced fairly quickly (Glutz et al. 1977). The African Snipe and the Madagascar Snipe appear to breed twice in a year. This is possible because of the high annual environmental productivity in tropical Africa where these birds breed.

Parental care varies between the various snipe species, with the majority having female care of the offspring. The African Snipe is monogamous and both parents take care of the young. It is not yet clear whether the parents share the task of incubating eggs and building the nest. In the Jack Snipe, Pintail Snipe and Great Snipe, females select nest sites, build the nests and incubate eggs while males guard them. While receptive females are guarded by breeding males early in the season, those males have opportunities to mate with other receptive females later, especially after the onset of egg-laying and incubation. The occurrence of 2 nestings in a season may enable the male African Snipe to maximize reproductive output by staying with one female.

Food and its acquisition

The diet of both the resident and Palearctic snipes is generally similar, consisting mainly of annelids, molluscs, insects, crustaceans and vegetable matter (Urban et al. 1986). Consumption of seeds is occasional but varies with habitat and season. The species of snipes with relatively short bills, especially Jack Snipe and Common Snipe, tend to consume more seeds and vegetable material than the species with longer bills (Devort et al. 1997). The African Snipe and the Madagascar Snipe which have relatively long bills eat predominantly invertebrates, especially earthworms.

Conservation status

Snipes are highly opportunistic and live in a wide range of wetland habitats. Areas that are conserved for more conspicuous waterfowl species, such as ducks, geese

and flamingos, are in most cases not suitable for snipes which at times inhabit small permanent wetlands or inconspicuous seasonal wetlands.

As a result of landscape modifications in Europe and northern Asia where Palearctic snipes breed, and also in Africa where they winter, the global populations of migrant snipes appear to be gradually declining due to loss of suitable habitats. The populations of the Great Snipe and Pintail Snipe, for instance, have decreased considerably both in Europe and Africa.

Habitat changes, due to changes in climate, drainage of wetlands and pollution of water systems, also threaten the survival of the African Snipe and Madagascar Snipe throughout their distribution ranges in the continent. Sport hunting of snipes poses no serious threat to the existence of this group of birds in Africa as the practice is largely uncommon.

Summary and conclusion

Snipes form a diverse group of waders that inhabit wetlands in various parts of the world. They have a strong association with moist or soft substrates from which they acquire food. The birds depend on their large and strategically placed eyes as well as their long and sensitive bill to detect food. The bills are weak and cannot penetrate hard surfaces. The males, females and juveniles are generally similar and well camouflaged. The birds are capable of rapidly "freezing" or taking off rapidly when disturbed or threatened by a predator.

The morphological adaptations, such as long bill, and long wings (relative to the size of the body) that permit rapid take-off, have contributed significantly to the survival and success of snipes in a wide range of wet or moist habitats in their northern breeding areas and wintering areas in Africa. The populations of the various snipes are not well documented but declines can be inferred from rapidly shrinking or deteriorating habitat. Annual counts of snipes carried out in Africa do not provide accurate data, or show any pattern of population changes.

There is considerable similarity in the food, breeding habitat and breeding behaviour of Palearctic and tropical snipes. Nearly all consume a wide variety of invertebrates and breed in wet and cool or cold environments. While Palearctic snipes make annual long-distance movements between their European breeding areas and wintering areas in Africa, the African Snipe and Madagascar Snipe make seasonal and altitudinal movements within their ranges.

The three sub-populations of African Snipe are separated by large areas of arid land, and as long as they remain isolated from each other by physical barriers they could evolve into different species. In this context, the Madagascar Snipe appears to be the remnant of a larger population that was widespread in Africa but long ago disappeared from the continent.

There is also a lack of variability in clutch size and nest site. The Palearctic and tropical snipes have similar clutch sizes and have retained the primitive ground-nesting habit of their presumably larger ancestors. A polygynous mating system and female parental care appear to be widespread among snipes. The evolution of monogamy in the African Snipe and the marked territorial behaviour of the Great Snipe and Jack Snipe appear to have been necessitated by high costs of parental care in the breeding areas of those species.

Greater attention in terms of research and conservation should be accorded to this complex and interesting group of waders. Snipes offer ample scope for research and opportunity for promoting conservation of shorebirds and the wetlands that support them. Snipes also provide useful tools for investigating various principles of ecology, evolutionary biology and sociobiology in animals.

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References

- Devort, M., F. Chevallier, H. Lethier, G. Olivier & J. Veiga (1997): The Snipe: Elements of an Action Plan. – Editions confluences, CICB, OMPO, Paris.
- Futuyma, D.J. (1979): Evolutionary Biology. – Sinauer Associates Inc., Sunderland, U S A.
- Gichuki, C. M., N.N. Gichuki & E.W. Kairu (1998): Population Biology and Breeding Ecology of the African Snipe *Gallinago nigripennis* in Central Kenya. – Proc. 5th Int. Woodcock and Snipe Conf., 3-5 May, 1998, Czempin, Poland.
- Glutz von Blotzheim, U., K.M. Bauer & E. Bezzel (1977): Handbuch der Vögel Mitteleuropas. Band 7 (Charadriiformes). – AULA Wiesbaden, Germany.
- Hayman, P., J. Marchant & P. Prater (1986): Shorebirds: an identification guide. – Beckenham; Croom Helm, UK.
- Moreau, E.R. (1972): The Palearctic African Bird Migration Systems. – Academic Press, London, New York.
- Perrins, C.M. & A.L.A. Middleton (eds). (1987). The Encyclopedia of Birds. – Equinox Ltd., Oxford.
- Reddig, E. (1978): Der Ausdrucksflug der Bekassine. – J. Ornithol. 119: 357-387.

- Sibley, C.G. & B.L. Monroe (1990): Distribution and Taxonomy of Birds of the World. – Yale University Press, New Haven, U S A.
- Urban, E.K., C.H. Fry & S. Keith (1986): Birds of Africa, vol. 2. – Academic Press, London .
- Zimmerman, D.A., D.A. Turner & D.J. Pearson (1996): Birds of Kenya and northern Tanzania. – Russel Friedman Books Halfway House, South Africa.

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Review of karyological studies and the problems of systematics of Ethiopian *Arvicanthis* Lesson, 1842 (Rodentia: Muridae)

M.I. Baskevich & L.A. Lavrenchenko

Abstract: A review of karyological research in rats of the genus *Arvicanthis* in Ethiopia together with new data on the karyotype and intrapopulational chromosomal variability (especially variations in the amount of heterochromatin in *A. somalicus* from Awash National Park) are given. The chromosomal characteristics of the species are evaluated in view of their divergence as a result of long historical isolation. The possible role of chromosomal peculiarities in forming and supporting the isolating mechanisms among semisympatric species is discussed. The hypothesis on the possible positive correlation between species age and chromosomal variability is tested in the genus *Arvicanthis*. Taxonomic aspects of the accumulated chromosomal data for Ethiopian *Arvicanthis* are discussed.

Key words: chromosomes, Muridae, *Arvicanthis*, variability, evolution, systematics, Africa, Ethiopia, endemics

Introduction

The present distribution of Grass rats of the genus *Arvicanthis* in Africa in different habitats (savanna, grassland, moorland, croplands and some others) reaches from the Nile basin, the Horn of Africa and East Africa across the central and western sub-saharan regions to West Africa. The history of the genus *Arvicanthis* in Africa started about 5 Mio years ago when the colonization of the continent from Asia took place (Jacobs 1978), and since that time the evolution and distribution of the genus has been significantly determined by climatic changes, leading to the isolation of populations over millions of years (Kingdon 1974). The results of these historical processes are obvious today on different levels, including that of the chromosomes.

We studied the chromosomal peculiarities in the genus *Arvicanthis* in Ethiopia, where four species are recognized: either *A. abyssinicus*, *A. blicki*, *A. somalicus* and *A. dembeensis* (Yalden et al. 1976, Corbet & Hill 1991) or the first three and *A. niloticus* (Musser & Carleton 1993).

While chromosomal differentiation is well documented for most Ethiopian representatives of the genus (Matthey 1959, Orlov et al. 1989, 1992, Baskevich et al. 1995, Corti et al. 1996, Lavrenchenko et al. 1997; see table 1) nothing was known about the karyotype of an endemic population in the Horn of Africa, *A. somalicus* – a small form adapted to low altitudes and dry climatic conditions (Yalden et al. 1976).

We studied the chromosomal sets of 5 specimens of *Arvicanthis* from Awash National Park (table 1) identified according to their upper tooththrow as *A. somalicus*.

Results

Within the studied specimens an intraspecific chromosomal polymorphism was obvious. Two specimens had a karyotype of 62, being composed of gradually decreasing acrocentrics, except one of the smallest pair of metacentric autosomes, and large submetacentric X- and medium-sized Y-chromosomes (NF=66). Following C-band staining all autosomes were revealed as medium-sized blocks of pericentromeric heterochromatin, Y-chromosome entirely heterochromatinized and X-chromosome strongly stained in its pericentromeric region, in the whole short arm and before the distal end of the long arm (fig.1). The remaining specimens had karyotypes with 62 chromosomes with rearrangements in the first (standard and increased homologues) (1 sp. - fig.2a) or in one of the medium-sized (acrocentric and subtelocentric homologues) (2 sp. - fig.3a) pairs of autosomes. (In the karyotype of one 62-chromosomal specimen with rearrangement in a medium-sized autosomal pair, a fusion of acrocentric autosomes seemed to occur and we preliminary reduced its diploid number; but more detailed investigation supported its 62-chromosome state). It became obvious that the mechanism of this chromosomal polymorphism is due to the variability in the amount of heterochromatin (fig. 2b, 3b). We suggest that the system of intraspecific chromosomal polymorphism caused by changes in the heterochromatin quantity has an adaptive significance.

When we compare our chromosomal results with published ones we can state that the 62-chromosome, un rearranged karyotype of *A. somalicus* is similar to that



Fig.1: Standard C-banded karyotype of *Avicanthis somalicus* ♀ from Awash National Park

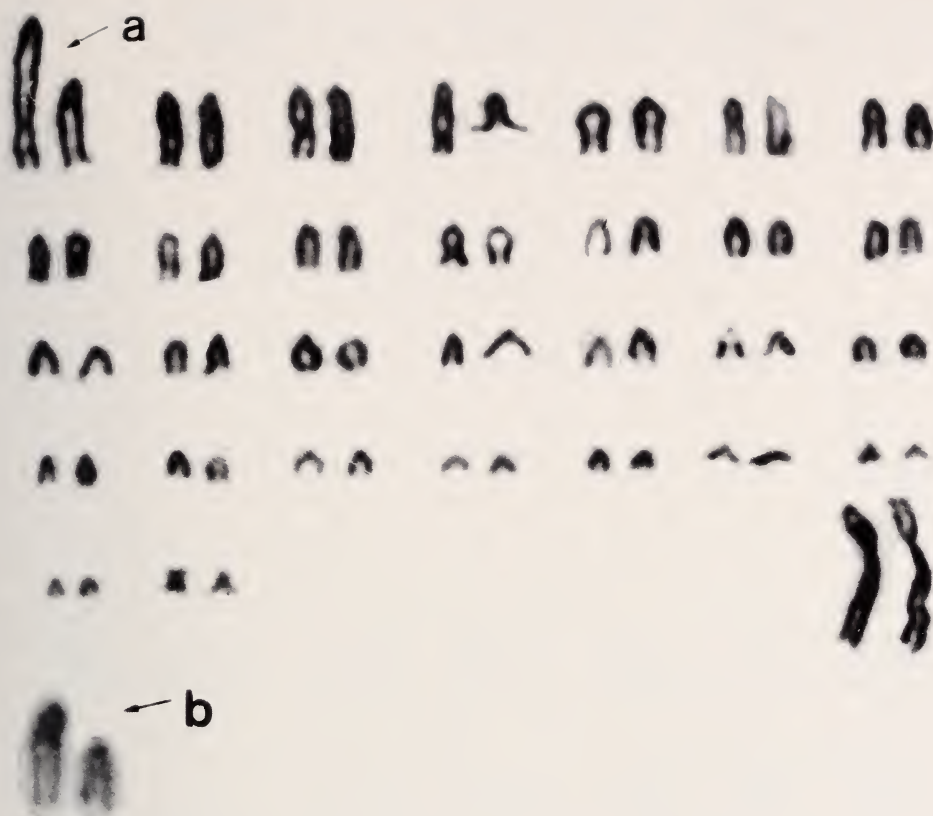


Fig.2: Karyotype of female *A. somalicus* with rearrangement in the 1st pair of autosomes: a: routine staining; b: C-band staining of the 1st pair

of *A. dembeensis*, found earlier at three localities in Ethiopia (Orlov et al. 1989, 1992, Baskevich et al. 1995, Corti et al. 1996; table 1). Obviously the same karyotype will be found in the specimens of *A. dembeensis* from Awash National Park where the ranges of these two species overlap (Yalden et al. 1976). We believe that the chromosomal peculiarities do not play an important role as an isolating mechanism among these sympatric species. But if they play a role in isolation their contribution is restricted to heterochromatin pattern only.

In addition to the 62-chromosome *A. dembeensis*, a 60-chromosome *Arvicanthis* (sp.1) and a 56-chromosome *Arvicanthis* (sp. 2) have been distinguished in Ethiopia (table 1), all representing the "morphotype" of *A. dembeensis*. The first one has been recorded in the south of the Ethiopian Rift Valley, the second coexists with the 62-chromosomes *A. dembeensis* in the Gambella area. Distinct karyological forms within the morphotype of *A. dembeensis* in different localities of Ethiopia seem to correspond to relict populations, isolated from the rest of the species by dry areas since the last wet period. This assumption agrees with the

Table 1: Karyotypes of Ethiopian *Arvicanthis*

Species/locality coordinates	habitat/altitude (m a.s.l.)	no. of specimens	2n	NF	X-	Y-	reference
<i>A. abyssinicus</i>							
1/unknown			62	64	Sm	A	Matthey 1959
2/ Ambo 8°56'N, 38°58'E	Cropland/ 2000	1	62	68	Sm	-	Orlov et al. 1989
8°56'N, 38°58'E	ditto	11	62	68	Sm	Sm	Orlov et al. 1992
3/Solulta 9°15'N, 38°43'E	cropland/ 2700	3	62	68	Sm	M	Corti et al. 1996
9°15'N, 38°43'E	ditto	2	62	68	St	M	Corti et al. 1996
4/Managesha 9°00'N, 38°35'E	<i>Combretum</i> savanna/2200-2300	5	62	68	Sm	M	Corti et al. 1996
<i>A. blicki</i>							
1/Bale Mts, Sanetti plateau 6°51'N, 39°52'E	alpine moorland/ 4000	1	48	68	Sm	-	Corti et al. 1996
2/Bale Mts, Sanetti plateau 6°51'N, 39°53'E	Afroalpine belt/4050	1	48	68	Sm		Lavrenchenko et al. 1997
<i>A. dembeensis</i>							
1/ Gambella 7°53'N, 34°22'E	<i>Combretum</i> savanna/450	5	62	66	Sm	M	Orlov et al. 1989, 1992
2/ 70 km N of Awash Nat. Park 9°28'N, 40°18'E	<i>Acacia</i> arid savanna/900	2	62	66	Sm		Orlov et al. 1992
3/ Koka 8°13'N, 38°55'E	open savanna, cropland/1550	20	62	66	Sm	M	Baskevich et al. 1995
4/ Koka 8°24'N, 39°01'E	open savanna/ 1650	3	62	66	Sm	M	Corti et al. 1996
<i>Arvicanthis</i> sp.1 Konso 5°25'N, 37°20'E	savanna/ 900	2	60	78	St	St	Orlov et al. 1992
<i>Arvicanthis</i> sp.2 Gambella 7°53'N, 34°22'E	<i>Combretum</i> savanna/450	1	56	60	A	A	Orlov et al. 1989
<i>A. somalicus</i> Awash Nat. Park 9°00'N, 40°10'E	<i>Acacia</i> arid savanna/900	5	62	66-67	Sm	M	this study

known relationship between *Arvicanthis* and humidity (see Kingdon 1974) and their recent distribution in Ethiopia (Yalden et al. 1976). Since chromosomal material from the *terra typica* of *A. dembeensis* (Tana lake area) is lacking, it is not possible to draw taxonomical conclusions for the various forms of "*dembeensis*". Additionally, species rank of *A. dembeensis* was confused in the last taxonomic



Fig.3: Karyotype of *A. somalicus* ♂ with rearrangement in the medium sized autosomal pair; a: routine staining; b: C-banding.

review (Musser & Carleton 1993) where it is considered as a junior synonym of *A. niloticus*.

A. abyssinicus and *A. blicki* are endemic to Ethiopia (Yalden & Largen 1992, Musser & Carleton 1993), thus indicating the isolation of Ethiopia over a

considerable period. Both species are adapted to higher altitudes on the Ethiopian plateau and to alpine grasslands, to which they may have been restricted during the upper Quaternary intertropical dry phase after the last glaciation (Adamson et al. 1980). They share a common ancestor and speciated during the Pleistocene (Corti et al. 1996). The analysis of chromosomal data for *A. abyssinicus* from three known localities ($2n=62$, $NF=68$) and *A. blicki* ($2n=48$, $NF=68$) reveals that their karyotypes are distinct (table 1): their differences consist of 7 Robertsonian translocations and similarities by the NORs localization pattern (Corti et al. 1996). Indeed, the specific localization of NORs in the two first pairs of autosomes - which are characteristic for only these two species - indicates on the chromosomal level that *A. abyssinicus* and *A. blicki* share a common ancestor. The variability in the X- and Y-chromosome morphology caused by changes in the amount of heterochromatin in the heterochromosomes and in the morphology of the two pairs of autosomes ($2n=62$, $NF=68$) characterizes the karyotype of *A. abyssinicus* (table 1).

It is known that *A. dembeensis* and *A. abyssinicus* diverged earlier than the Ethiopian endemics (Capula et al. 1996, cit. from Corti et al. 1996). The karyotype of *A. abyssinicus* differs from that of the 62-chromosome *A. dembeensis* by one pericentromeric inversion (Corti et al. 1996) and from that of the 60-chromosome *Arvicanthis* sp. 1 ("morphotype" *A. dembeensis*) by one Robertsonian translocation, four pericentric inversions and four chromosomal rearrangements connected with heterochromatin variations (Orlov et al. 1992).

When we compare the karyotypes of the Ethiopian species and estimate their chromosomal variability we see the conservative structure of the sex chromosomes in the four Ethiopian species (Orlov et al. 1989, 1992, Baskevich et al. 1995, Corti et al. 1996; our data). The last observation can support the monophyly of the Ethiopian group.

It has been shown that *A. blicki* is the most recent species in the genus *Arvicanthis*. Its divergence from the genetically related *A. abyssinicus* is dated to the end of Pleistocene; the latter diverged earlier from *A. dembeensis*; the time of divergence between West and East African lineages of *Arvicanthis* has been estimated to the Upper Pliocene (Capula et al. 1996, cit. from Corti et al. 1996). Using these data we can try to test the hypothesis of a positive correlation between the age of a taxon and its chromosome variability (Gileva 1990). The chromosome variability in Ethiopian *Arvicanthis* as demonstrated in table 1 and the age of the genus supports this assumption.

When we summarize the chromosomal results on Ethiopian *Arvicanthis* we can state that the number of known chromosomal forms exceeds the recognized species number (Yalden et al. 1976, Musser & Carleton 1993); therefore it is possible that future revisions of this genus may increase the number of species and thus the Ethiopian theriofauna.

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References

- Adamson, D.A., F. Casse, F.A. Street & M.A.J. Williams (1980): Late Quarternary history of the Nile. – *Nature*, London 288: 50-55.
- Baskevich, M.I., V.N. Orlov, A. Bekele & A. Mebrate (1995): New data on the karyotypes of Ethiopian small mammals (Insectivora, Rodentia). – pp. 58-72 in: *Theriological studies in Ethiopia* (ed. Sokolov, V.E.). – Nauka, Moscow.
- Corbet, G.B. & J.E. Hill (1991): *A world list of mammalian species*. – Oxford University Press, Oxford.
- Corti, M., M.V. Civitelli, R. Castiglia, A. Bekele & E. Capanna (1996): Cytogenetics of the genus *Arvicanthis* (Rodentia, Muridae). 2. The chromosomes of three species from Ethiopia: *A. abyssinicus*, *A. dembeensis* and *A. blicki*. – *Z. Säugetierk.* 61: 339-351.
- Gileva, E. A. (1990): *Chromosomal variability and evolution*. – Nauka, Moscow, 141 pp.
- Jacobs, L. (1978): Fossil rodents (Rhizomyidae and Muridae) from Neogene Siwalik deposits, Pakistan. – *Bull. Mus. North. Arizona Press* 52: 1-103.
- Kingdon, J. (1974): *East African Mammals: an atlas of evolution in Africa*. Vol. II, part. B: hares and rodents. – Academic Press, London.
- Lavrenchenko, L.A., A.N. Milishnikov, V.M. Aniskin, A. A. Warshavsky & W. Gebrekidan (1997): The genetic diversity of small mammals of the Bale mountains, Ethiopia. – *SINET: Ethiop. J. Sci.* 20: 213-233.
- Matthey, R. (1959): Formules chromosomiques de Murinae et de Spalacidae. La question du polymorphisme chromosomique chez les Mammifères. – *Rev. Suisse Zool.* 66: 175-209.
- Musser, G.G., M. D. Carleton (1993): Family Muridae. – pp. 501-755 in: *Mammal Species of the World. A taxonomic and geographic reference* (eds. Wilson, D.E. & D.M. Reeder) – Smithsonian Inst. Press, Washington, London.
- Orlov, V.N., M.I. Baskevich & N.Sh. Bulatova (1992): Chromosomal sets of the rats of the genus *Arvicanthis* from Ethiopia. – *Zool. Zh.* 71: 103-112.
- Orlov, V.N., N. Sh. Bulatova & A.N. Milishnikov (1989): Karyotypes of some mammalian species (Insectivora, Rodentia) in Ethiopia. – pp. 72-94 in: *Ecological and Faunistic studies in South-Western Ethiopia*. – Nauka, Moscow.
- Yalden, D.W., M.J. Lagen & D. Kock (1976): *Catalogue of mammals of Ethiopia*. 2. Insectivora and Rodentia. – *Monit. Zool. Ital. (NS)*, suppl. 8: 1-118.
- Yalden, D.W. & M. J. Lagen (1992): The endemic mammals of Ethiopia. – *Mammal Rev.* 22: 115-150.

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Isolation of bird populations in the North Nandi Forest, western Kenya

Herbert Schifter

Abstract: The North Nandi Forest is inhabited by some clearly isolated populations of small passerines which have been given subspecific rank only recently (Cunningham-van Someren & Schifter 1981). These include *Phyllastrephus cabanisi*, *Bleda syndactyla*, *Sheppardia aequatorialis pallidigularis*, *Alethe poliocephala*, *Cossypha cyanocampter*, *Neocossyphus poensis*, *Turdus olivaceus porini* and *Illadopsis abyssinica*. Some of them have been generally acknowledged. Indeed some isolated populations which have not yet been named as separate subspecies may exist. Among them the population of *Zosterops senegalensis*, should be mentioned, which is certainly intermediate between the populations to the east and those in the lower-lying Kakamega Forest. Also *Pogonochila stellata* of the North Nandi Forest differs markedly from the population of the Mount Elgon area to the west. Furthermore there exists a very marked population of *Platysteira concreta*, which was formerly known only from the Kakamega Forest, therefore supporting extended protection of both areas. By contrast, larger birds seem to move regularly from the North Nandi Forest and do not represent isolated populations, but conservation of the North Nandi Forest is also important for their protection.

Key words: Nandi forest, Kenya, new subspecies, conservation

The study area

The North Nandi Forest is an isolated forest in western Kenya which today is reduced to a narrow strip at the western edge of the North Nandi Escarpment, stretching about 32 km from north to south but only roughly 9 km wide. It ranges from about 1950 to more than 2150 m and is separated from the lower-lying and more western Kakamega Forest by the North Nandi Escarpment. The forest has been extensively logged in the past and has been widely cleared, mostly on its western edge. Only a small part of the forest has been declared as a Nature Reserve, in 1968 and in 1978. Nevertheless the remaining parts of the forest still house a great variety of animals and plants, though the number of species is lower than in the better known Kakamega Forest probably due to the greater altitude.

Birds in general

Among the resident bird species some have been found to represent obviously isolated populations, and have been given the rank of subspecies (Cunningham-van Someren & Schifter 1981), whereas larger birds undertake movements to the other forests in the area, especially the Kakamega Forest.

The isolated populations of smaller passerines which have been given subspecific rank are:

Olive Greenbul *Phyllastrephus cabanisi nandensis*
 Common Bristlebill *Bleda syndactyla nandensis*
 Equatorial Akalat *Sheppardia aequatorialis pallidigularis*
 Brown-chested Alethe *Alethe poliocephala nandensis*
 Blue-shouldered Robin-Chat *Cossypha cyanocamptor pallidiventris*
 White-tailed Ant-Thrush *Neocossyphus poensis nigradorsalis*
 Northern Olive Thrush *Turdus olivaceus porini*
 African Hill Babbler *Illadopsis abyssinica poliothorax*.

Some of them have been generally acknowledged. Indeed isolated populations which have not yet been named as separate subspecies, may exist. Among them is the population of the Yellow White-eye *Zosterops senegalensis*, which is certainly intermediate between the populations to the east and those in the lower-lying Kakamega Forest. Also the White-starred Robins *Pogonocichla stellata* of the North Nandi Forest differ markedly from the population of the Mount Elgon area to the west. Furthermore there is a very marked population of the Yellow-bellied Wattle-eye *Platysteira concreta*, which was formerly known only from the Kakamega Forest, which therefore supports extended protection of both areas. Larger birds which seem to move regularly from the North Nandi Forest to the Kakamega Forest do not represent isolated populations but conservation of the North Nandi Forest is important for their protection.

Selected bird species

The Common Bristlebill (*Bleda syndactyla*) is an inhabitant of the forests of West and Central Africa, reaching in western Kenya its eastern limit of distribution. Formerly included in the widespread subspecies *B. s. woosnami*, the Kenyan population has been separated as *B. s. nandensis* by Cunningham-van Someren & Schifter (1981) mainly because of its larger size. It is a rare species in North Nandi, reaching here its upper limit of distribution. Also the Nandi population of the Olive Greenbul (*Phyllastrephus cabanisi*) has been separated as *P. c. nandensis* by its more greenish back. Formerly included in *Phyllastrephus fischeri*, the highland populations have been merged recently into *P. cabanisi* (Dowsett 1972, Short et al. 1990: 154).

The Equatorial Akalat *Sheppardia aequatorialis* is one of the common birds of the forest undergrowth. The population of the North Nandi Forest is different from those of other highland forests in Kenya and therefore has been separated as *Sheppardia aequatorialis pallidigularis* by being more "golden-yellow" than brown, with a conspicuous pale throat. Specimens from the Kakamega are darker without the distinct pale throat. Nevertheless both populations have been merged with the nominate subspecies by Fry et al. (1992). Many subadult birds caught between October and December in the study area indicate breeding late in the year in the North Nandi Forest whereas no subadult birds were found in September 1988.

The Brown-chested Alethe (*Alethe poliocephala*) is a mostly West and Central African species of the family Turdidae. The population of the North Nandi Forest has been separated as *Alethe poliocephala nandensis*, based on the more pronounced Brussels brown of the back and also by its lack of a marked breast

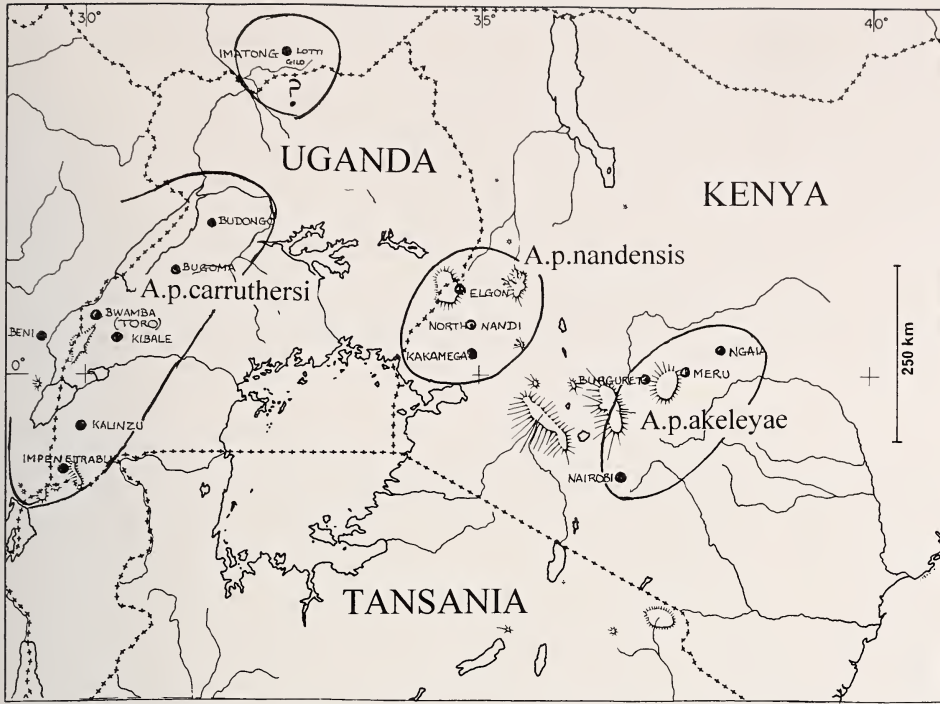


Fig. 1: Distribution of the subspecies of *Alethe poliocephala* in eastern Africa

band, from the more eastern subspecies *A. p. akeleyae*. Though a very common species of the forest undergrowth, this alethe seems to be very sedentary, as shown by a specimen ringed as an adult bird on 23 November 1979 which was retrapped at a distance of only 100 m from the ringing site nearly nine years later on 21 September 1988 (Gichuki & Schifter 1990).

The White-tailed Ant-Thrush (*Neocossyphus poensis*) of the North Nandi Forest has been separated as *N. p. nigridorsalis*. Though a rare bird in the area and confined to wetter parts near streams and swamps the bird seems to be very sedentary. The population of the Kakamega Forest has also been recently separated as *N. p. kakamegoes* by Cunningham-van Someren & Schifter (1981). Similarly, the clearly isolated population of the Northern Olive Thrush (*Turdus olivaceus*) might be separable as *T. o. porini*, differing even from nearby *T. o. elgonensis* by darker breast and back. Generally the populations of the Northern Olive Thrush in Kenya are certainly different from *T. abyssinicus* of the Ethiopian highlands.

The Blue-shouldered Robin-Chat (*Cossypha cyanocampter*) also is a West and Central African species reaching its eastern limit of distribution in the North Nandi Forest. The resident birds of the forest have been named *C. c. pallidiventris*, though this separate population is not generally acknowledged and has been merged recently again with *C. c. barteloti* by Fry et al. (1992). The Nandi Forest population of the White-starred Robin (*Pogonochila stellata*) may also represent

a distinct subspecies but has usually been included in the wider-ranging *P. s. intensa*. It should be noted that the nearby Mount Elgon is inhabited by its own subspecies *P. s. elgonensis*.

The North Nandi population of the widespread African Hill Babbler (*Illadopsis abyssinica* [?]) has been separated as *Alcippe a. poliothorax* by its paler ventral surface. The distribution of the species, occurring in isolated mountain islands, is highly discontinuous in East Africa with even more significantly distinct populations in areas such as Mt. Loima in western Turkana. Therefore Hill Babblers from Kenya (formerly included in *Alcippe*) should certainly not be merged with the nominate subspecies from Ethiopia. Other Timaliidae of the North Nandi Forest belong to Central African species and may not be separable from the more westerly populations, including the rare Gray-chested Illadopsis *Kakamega poliothorax*.

The Yellow-billed [oder bellied?] Wattle-eye (*Platysteira concreta*) is also a West and Central African species. It was discovered in western Kenya only in 1923 and this population was named *P. c. silvae* by Hartert & Van Someren. In the North Nandi Forest it was discovered only in 1978 by our expedition (see also Schifter & Cunningham-van Someren 1998) where it is also obviously a rare bird. The isolated populations of western Kenya are likely to represent a separate subspecies as listed by Zimmerman (1972), though not generally acknowledged probably due to the very limited material available for studies in museum collections. Occurrence of the Yellow-bellied[s.o.!] Wattle-eye in North Nandi Forest, as well as the endemic subspecies of the area, strongly indicate that the site requires improved protection.

The Black-throated Wattle-eye (*Platysteira mentalis*) and Jameson's Wattle-eye (*Platysteira jamesoni*) of the North Nandi Forest probably do not represent separable subspecies. Migratory species such as the African Paradise Monarch-Flycatcher (*Terpsiphone viridis*) are not represented by distinct subspecies; in this species two different subspecies (*T. v. suahelica* and *T. v. ferreti*) have been confirmed by mistnetting. Also tits and sunbirds found in the North Nandi Forest do not differ significantly from populations found in the Kakamega Forest or in the highlands of Central Kenya. Yellow White-eyes (*Zosterops senegalensis*) are very common in the North Nandi Forest. Specimens of the probably resident population differ only slightly from those from the type locality of *Z. jacksoni* (Mau) and are intermediate between them and the more western *Z. yalensis* (named by Van Someren from Kaimosi). There is also considerable individual variation. Therefore the birds of the North Nandi Forest should still be included in *Zosterops senegalensis jacksoni* as long as further studies do not support new taxonomic views.

References

- Cunningham-van Someren, G.R. & H. Schifter (1981): New races of montane birds from Kenya and southern Sudan. – Bull. Brit. Orn. Cl. 101: 347-354, 355-363.
- Dowsett, R.J. (1972): Is the bulbul *Phyllastrephus placidus* a good species? – Bull. Brit. Orn. Cl. 92. 132-138.

- Fry, C.H., Keith, S. & Urban, E.K. (1992): The birds of Africa. Vol. IV.– Academic Press, London.
- Gichuki, C.M. & H. Schifter (1990): Long life-span and sedentariness of birds in North Nandi Forest, Kenya. – *Scopus* 14. 24-25.
- Schifter, H. & G.R. Cunningham-van Someren (1998): The Avifauna of the North Nandi Forest, Kenya. – *Ann. Nat.hist. Mus. Wien* 100B: 425-479.
- Short, L.L., J.F.M. Horne & C. Muring-Gichuki (1990): Annotated check-list of the birds of East Africa. – *Proc. West. Foundation of Vertebrate Zoology*, 4 (3): 61-246.
- Zimmerman, D.A. (1972): The Avifauna of the Kakamega Forest, Western Kenya, including a bird population study. – *Bull. Amer. Mus. Nat. Hist.* 149 (3). 255-340.

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The mammals of the isolated Harennā Forest (southern Ethiopia): structure and history of the fauna

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Abstract: The results of the faunistic survey of mammals conducted in the Harennā Forest are given. Seven mammalian species were recorded for the first time for the forest, two of them (*Stenonycteris lanosus* and *Dasyms incontus*) were new for the whole area to the east of the Ethiopian Rift Valley. Altogether fifty-three mammalian species (including three species endemic to the forest) are so far known from the Harennā Forest. Distribution of mammals along an elevational gradient was studied. On the whole, the relationship between species-richness and elevation is strikingly hump-shaped, peaking in the 1900 – 2500 m zone. Furthermore, elevational ranges do not tend to increase with elevation, so “Stevens’s rule” is not corroborated. This effect may be associated with the absence of specialised low-elevation species as a result of the isolated position of the forest. In general, the mammalian fauna of the Harennā Forest was formed rather recently, mainly through a limited immigration of forest species and recruitment of species from adjacent altitudinal zones with their subsequent adaptive speciation. Although the fauna of the Harennā Forest demonstrates a superficial similarity with other African forest faunas, sharing with them such specialised ecological forms as forest guenon and arboreal hyrax, it is to a large extent unrelated to these mammalian faunas phylogenetically.

Key words: biogeography, forest mammals, elevational gradient, endemics, Ethiopia

Introduction

The southern slope of the Bale Mountains represents a continuous range of undisturbed natural vegetation, from 1500 to 4400 m a.s.l. Such an environment is found in very few, if any, montane terrains in Africa. Montane evergreen tropical rain forest, known locally as the Harennā Forest, encompasses the largest part of this area (from 1500 to 3250 m a.s.l.). Furthermore, this forest is separated from other forest areas by the Rift Valley to the west, the flat high Sanetti Plateau to the north, and arid lowlands on the other sides. This makes the Harennā Forest a valuable model for the study of formation and evolution of an isolated tropical forest fauna.

Until recently, the mammalian fauna of this forest was unexplored. The first zoological expedition reached the Harennā Forest only in August 1986 and found there three species new for Ethiopia (*Cercopithecus albogularis*, *Cephalophus ?harveyi* and *Mus* cf. *triton*) and two species new to science (*Crocidura harennā* and *Crocidura bottegoides*) (Afework Bekele 1988, Yalden 1988a, b, Hutterer & Yalden 1990, Yalden et al. 1996). It is likely that more undiscovered mammals occur in this forest. Furthermore, the Harennā Forest is an important but poorly known part of the Bale Mountains National Park (BMNP), which is one of the few

protected key areas in Ethiopia. So, basic information on mammalian fauna of this forest is of importance for local conservation projects.

This paper presents the results of the faunistic survey of mammals conducted along an elevational transect in the Harennna Forest between February 1995 and January 1996. A biogeographical analysis of these findings and the resulting patterns of altitudinal zonation of the mammalian fauna are also given.

Study area and methods

As a result of the great altitudinal range both, structure and composition of the Harennna Forest vary significantly. The following major vegetation belts have been visually recognized:

- 1) *Podocarpus* belt (1550 – 1900 m a.s.l.)
- 2) *Aningeria* belt (1900 – 2350 m)
- 3) *Schefflera* – *Hagenia* belt (2350 – 2600 m)
- 4) *Hagenia* – *Schefflera* – *Hypericum* belt (2600 – 3000 m)
- 5) *Hypericum* – *Erica* – *Rappanea* belt (3000 – 3250 m) (Lisanework Nigatu & Mesfin Tadesse 1989).

A trapping-line of 100 live-traps was placed in each of these vegetation belts to study the distribution of small rodents and shrews (for detailed description of the trapping sites, see Lavrenchenko et al. 1998). Bats were caught in mist nets, positioned in clearings in the forest near these sites. Vehicle monitoring along the road, crossing the Harennna Forest, was carried out to study the distribution of the larger species. Additionally notes, measurements and photographs were made of any tracks, burrows and droppings of medium-sized and large mammals. I also used published records for the forest (Afework Bekele 1988, Yalden 1988a, b, Hutterer & Yalden 1990, Yalden et al. 1996) and unpublished data from archival files of the Bale Mountains National Park.

The elevational range of each species was calculated. For most species it was determined by interpolating between elevational extremes (with the exception of few species – *Crocidura thalia*, *C. olivieri*, *Dendromys mystacalis*, and *Stenocephalemys griseicauda* – inhabiting only ericaceous bush near the upper limit of the forest and/or riverine habitats inside the forest). The elevational transect was divided into 18 arbitrarily defined 100-m units. A species was considered to be inhabiting an elevational unit if its altitudinal range covered more than a third of this unit. Similarities among species assemblages in these units, and turnover rates between adjacent zones on the elevational gradient, were evaluated by Jaccard's coefficient (J) using the NTSYS program (Rohlf 1988).

Results and discussion

In total, fifty-three mammalian species were recorded in the Harennna Forest (table 1). Seven species (*Rousettus aegyptiacus*, *Stenonycteris lanosus*, *Miniopterus schreibersi*, *Heterohyrax brucei*, *Heliosciurus gambianus*, *Lophiomy's imhausii*, and *Dasymys incommutus*) were recorded for the first time for the forest, two of them (*Stenonycteris lanosus* and *Dasymys incommutus*) were new for the whole area east of the Ethiopian Rift Valley. Furthermore, our study has revealed that *Lophuromys*

Table 1. – Species of mammals recorded in the Harenna Forest.

Zoogeographic categories modified from Yalden et al. (1996): CAF = Central African forest, EAF = East African forest, EAM = East African montane, EAS = East African savanna, EE = endemic to Ethiopia, EH = endemic to the Harenna Forest, P = Palearctic, PAS = Pan-African savanna, SA = Somali-arid, SS = Saharo-Sindian, WAS = West African savanna, U = unclassified.

No.	Species	Zoogeographic category	Habitat in the Harenna Forest	Range of records (m)
1	<i>Crocridura thalia</i>	EE	grassland	1 935-3 300
2	<i>Crocridura olivieri</i>	PAS	grassland	1 935-2 400
3	<i>Crocridura bottegoides</i>	EE	forest/grassland	2 400-3 280
4	<i>Crocridura harenna</i>	EH	forest	2 400-2 630
5	<i>Rousettus aegyptiacus</i>	U	forest	1 970
6	<i>Lissonictes angolensis</i>	CAF	forest	1 550-1 880
7	<i>Stenonycteris lanosus</i>	EAM	forest	1 970
8	<i>Rhinolophus cf. deckenii</i>	U	forest	1 970
9	<i>Rhinolophus clivosus</i>	U	woodland	1 530
10	<i>Rhinolophus landeri</i>	PAS	woodland	1 550
11	<i>Rhinolophus hildebrandtii</i>	EAS	forest	2 400
12	<i>Pipistrellus nanus</i>	PAS	forest	1 950
13	<i>Plecotus austriacus</i>	P	forest	1 980-3 280
14	<i>Miniopterus inflatus</i>	U	forest	1 950-3 280
15	<i>Miniopterus schreibersi</i>	U	forest	2 400
16	<i>Galago senegalensis</i>	WAS	forest	1 530-1 950
17	<i>Papio anubis</i>	WAS	grassland/forest	1 500-2 900
18	<i>Cercopithecus djamdjamensis</i>	EH	forest	2 400-2 800
19	<i>Colobus guereza</i>	CAF	forest	1 550-3 000
20	<i>Lycan pictus</i>	PAS	grassland	1 550-2 400
21	<i>Canis aureus</i>	SS	grassland/forest	1 680-2 400
22	<i>Viverra civetta</i>	U	forest/grassland	1 600-2 600
23	<i>Genetta maculata</i>	U	forest	1 900-2 400
24	<i>Atilax paludinosus</i>	U	forest	2 760
25	<i>Herpestes sanguineus</i>	U	forest	1 650-2 220
26	<i>Ichneumia albicauda</i>	PAS	forest/grassland	1 500-3 075
27	<i>Crocota crocuta</i>	PAS	forest/grassland	1 950-2 400
28	<i>Felis serval</i>	PAS	grassland/forest	1 680-2 400
29	<i>Panthera pardus</i>	U	forest	1 680-2 400
30	<i>Panthera leo</i>	U	forest/grassland	1 750-2 400
31	<i>Heterohyrax brucei</i>	EAS	forest	2 460-2 760
32	<i>Orycteropus afer</i>	PAS	woodland	1 550
33	<i>Hylochoerus meinertzhageni</i>	CAF	forest	1 600-2 400
34	<i>Potamochoerus larvatus</i>	EAF	forest/grassland	1 600-2 760
35	<i>Phacochoerus africanus</i>	PAS	grassland	2 350
36	<i>Sylvicapra grimmia</i>	PAS	forest/grassland	2 400-3 300
37	<i>Cephalophus ?harveyi</i>	EAF	forest	2 400
38	<i>Tragelaphus buxtoni</i>	EE	forest/grassland	2 140
39	<i>Tragelaphus scriptus</i>	U	forest	1 500-3 200

No.	Species	Zoogeographic category	Habitat in the Haremma Forest	Range of records (m)
40	<i>Heliosciurus gambianus</i>	PAS	forest	1 950-2 150
41	<i>Lophiomy's inhausii</i>	U	forest	2 760
42	<i>Dendromys mystacalis</i>	PAS	grassland	2 400-3 280
43	<i>Tachyoryctes splendens</i>	EAM	grassland	2 400-2 790
44	<i>Mus mahomet</i>	EAM	grassland	1 950-1 970
45	<i>Mus cf. triton</i>	EH	forest	1 950-2 920
46	<i>Praomys albipes</i>	EE	forest	1 500-3 075
47	<i>Stenocephalemys griseicauda</i>	EE	grassland	2 400
48	<i>Lophuromys brevicaudus</i>	EE	forest	2 400-3 300
49	<i>Lophuromys chrysopus</i>	EE	forest	1 550-2 760
50	<i>Dasymys incontinus</i>	PAS	swamp	1 970
51	<i>Graphiurus murinus</i>	PAS	forest	3 280
52	<i>Hystrix cristata</i>	WAS	forest/grassland	1 900-2 350
53	<i>Lepus habessinicus</i>	SA	grassland	2 400

"flavopunctatus" from the Haremma Forest comprises two distinct species, *L. brevicaudus* and *L. chrysopus*, both endemic to Ethiopia (Lavrenchenko et al. 1998).

The relationship between species-richness and elevation is strikingly hump-shaped, with a peak in the 1900-2500 m zone (fig.1). It is in agreement with the model of bounded random geographical ranges with two hard boundaries (model 4 in Rahbek 1997) where the pattern of species richness is produced on the assumption of random elevational association between the size and placement of

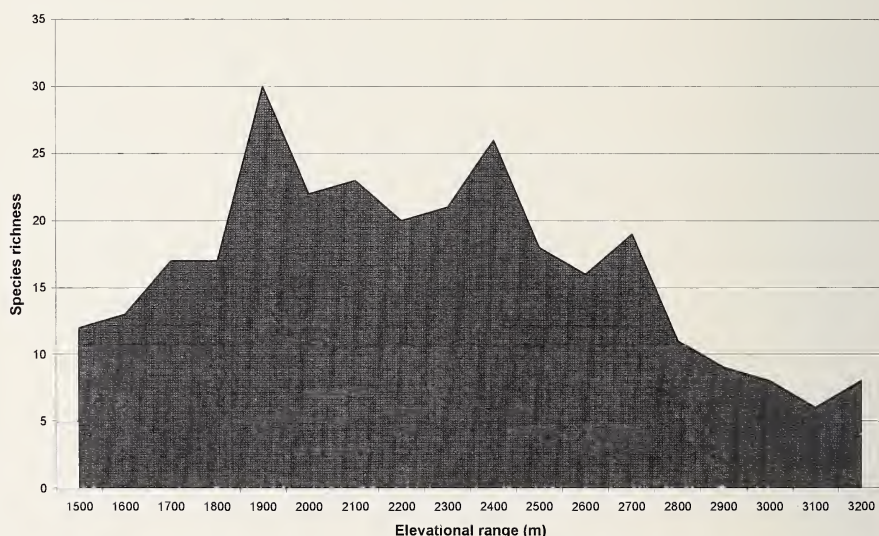


Fig.1: Elevational variation in the mammal species richness in the Haremma Forest.

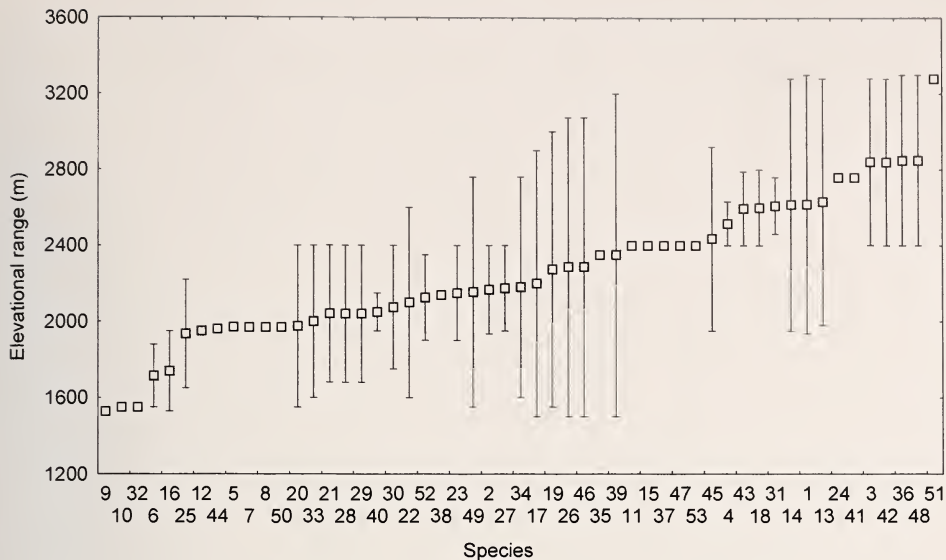


Fig.2: Elevational ranges (ordered by elevational midpoint) of mammal species of the Haremma Forest. See table 1 for numbers of species.

the species' elevational ranges. On the other hand, the hypothesis of a hump-shaped relationship between species-richness and primary productivity (model 3 in Rahbek 1997) cannot be rejected because in our case the peak was reached at an elevation lower than the median of the gradient.

Furthermore, elevational ranges do not tend to increase with elevation (fig.2). There is no significant correlation between the elevational range and the elevational midpoint ($r = 0.202$), so Stevens's (1992) extension of "Rapoport's rule" on the elevational gradient is not corroborated. It may be associated with the absence of specialised low-elevation species due to the isolated position of the forest. It is noteworthy that three forest species endemic to the Haremma Forest (*Crocidura haremma*, *Cercopithecus djamdjamensis* and *Mus cf. triton*) occur at medium elevations only, whereas more widespread Ethiopian woodland endemics (*Tragelaphus scriptus meneliki*, *Praomys albipes*, and *Lophuromys chrysopus*) show relatively broader altitudinal ranges in the forest. Jaccard's similarity profile for the Haremma Forest elevational gradient is given in fig.3. The two lowest dips in pairwise similarity (1900 m and 2400 m), indicating high turnover rate in mammalian species composition, correspond to the zone boundaries between the *Podocarpus* and *Aningeria* belts, and the *Aningeria* and *Schefflera-Hagenia* belts respectively. Therefore the biomes of these three vegetation belts possess to some extent discrete mammalian communities.

A characteristic feature of the Haremma Forest mammalian fauna is the nearly complete absence of both West and Central African forest species, which, however, occur in montane forests of south-west Ethiopia (*Crocidura niobe*, *Hypsignathus monstrosus*, *Epomophorus gambianus*, *Micropteropus pusillus*, *Hipposideros ruber*, *Hipposideros fuliginosus*, *Pipistrellus tenuipinnis*, *Mimetillus moloneyi*,

Mops nanulus, *Cercopithecus mitis boutourlinii*, *Cercopithecus neglectus*, *Oenomys hypoxanthus*) and of species found in riverine forests of southern Somalia (*Epomophorus wahlbergi*, *Nycteris parisii*, *Pipistrellus eisentrauti*, *Galago crassicaudatus*, *Cercopithecus mitis zammaranoi*). The Central African forest species *Lissonycteris angolensis* and *Hylochoerus meinertzhageni*, and the East African *Cephalophus harveyi*, are the exceptions (the occurrence of the latter species is supported by sightings only – for details see Yalden et al. 1996). Most of the forest species endemic to Ethiopia (*Crocidura macmillani*, *C. phaeura*, *C. zaphiri*, *Grammomys minnae*, *Desmomys harringtoni*, and *Praomys ruppi*) are absent from the Harennna Forest. The exceptions are two widespread Ethiopian forest endemics, *Praomys albipes* and *Lophuromys chrysopus*, for which a recent origin from aboriginal species of the ericaceous belt in the Bale Massif (*Lophuromys brevicaudus* and *Stenocephalemys griseicauda* respectively) has been proposed (Lavrenchenko et al. 2000). The contemporary distribution of these two species may be accounted for by dispersion from the Bale Massif during some periods in the Pleistocene when a more humid climate could have allowed the few forest and marsh species to spread across the Rift Valley, which at present is the major zoogeographic barrier in Ethiopia. Our finding of a relict and isolated population of *Dasymys incomtus* in a small swamp on the Shawe river in the centre of the Harennna Forest supports this hypothesis, assuming at the same time that the latter species could have dispersed in the opposite direction. Such relict populations of *Dasymys incomtus* are also known from Western Senegal (Duplantier et al. 1997).

The lack of widespread forest-dwelling, small terrestrial mammals for which the risk of local extinction and the colonising capacity is low, as well as the presence of some Central and East African forest ungulates (with the opposite characteristics), support the concept that the mammalian fauna of the Harennna Forest was formed rather by colonization *de novo* than by the extinction of representatives of a forest fauna once common in the whole of Central and East Africa.

On the other hand, the Harennna Forest is remarkable for the number of endemic mammals (*Crocidura harennna*, *Cercopithecus djamdjamensis* and *Mus* cf. *triton*) that inhabit this relatively small geographic area. *Crocidura harennna* is a typical member of a putative phylogenetic cluster of 36-chromosome *Crocidura* species from the Bale Massif. It is worth mentioning that the karyotype of this morphologically distinct species is practically identical with that of the montane Ethiopian endemic *Crocidura glassi* (Lavrenchenko et al. 1997).

The other Harennna endemic, *Cercopithecus djamdjamensis*, being a member of the superspecies *C. aethiops*, is uniquely adapted to closed-canopy montane forest (Carpaneto & Gippoliti 1994). Its resemblance to *C. mitis* sensu lato, possibly resulting from this adaptation, is so amazing that a single female, collected in the course of the Harennna Forest Expedition in 1986, was identified as *C. albogularis* (Afework Bekele 1988). However, our repeated observations of these monkeys confirm the conclusion of Carpaneto & Gippoliti (1994) that *C. djamdjamensis* belongs to the *C. aethiops* species complex, but not to the *C. mitis-albogularis* lineage (peculiarities of acoustics, locomotion and scrotum colour are the diagnostic features).



Fig.3: Pairwise Jaccard's similarities of mammal assemblages between adjacent elevational units of the Harennia Forest.

The distinctive, olive-brown *Mus* from the Harennia was assigned to *M. triton* (Yalden 1988 a). However, our detailed cytogenetic study (Aniskin et al. 1998) does not support this identification. Moreover, *Mus* cf. *triton* from the Harennia Forest, together with the widespread Ethiopian *M. mahomet*, belongs to the cytotaxonomic group that does not include the true *M. triton* and is characterised by primitive acrocentric heterochromosomes (for review, see Capanna 1985). So, all three endemic Harennia species originated apparently from aboriginal non-forest stocks and their resemblance to some species from other forest territories might be a result of convergence.

Further, the arboreal browser *Heterohyrax brucei* found in the Harennia Forest occupies the ecological niche of a *Dendrohyrax* species. A comparison with sizable material in the Koninklijk Museum voor Midden-Afrika (Tervuren) reveals that the Harennia *Heterohyrax* resembles *Dendrohyrax arboreus* in teeth pattern (but possesses the other main diagnostic cranial features of *Heterohyrax*), which may be a result of this ecological shift. It is noteworthy that Kingdon (1971) assumed a direct origin of *Dendrohyrax validus* from some ancestral *Heterohyrax* population. The Harennia Forest is the southernmost limit for the essentially Palaearctic species *Plecotus austriacus*. It is interesting that the Harennia *Plecotus* differs strikingly in its colour pattern from the neighbouring Arabian – North African subspecies *christii* and resembles conspecific specimens from more humid European areas.

It thus seems clear that the mammalian fauna of the Harennia Forest was formed rather recently and mainly through two different processes: a limited immigration of forest species and the recruitment of species from adjacent altitudinal zones (savanna and moorland) with their subsequent adaptive speciation. Apparently, the

latter process prevailed being promoted both by an ecological vacuum in the forest communities and richness of the non-forest Ethiopian fauna. The degree of the adaptation to forest habitats varies among representatives of different groups, reaching its ultimate expression in the three species endemic to this forest (and *Heterohyrax brucei*) found in the rather narrow altitudinal range most distant from the forest margins. These adaptations result in convergence with forest species from the rest of Africa.

Although the fauna of the Haremma Forest demonstrates superficial similarity with other African forest faunas, sharing with them such specialised ecological forms as Forest guenon and Arboreal hyrax it is to a large extent not related to these mammalian faunas.

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References

- Afework Bekele (1988): A census of large mammals in the Haremma Forest, Ethiopia. – *Sinet: Ethiop. J. Sci.* 11: 27-39.
- Aniskin, V.M., L.A. Lavrenchenko, A.A. Varshavskii & A.N. Milishnikov (1998): Karyotypes and cytogenetic differentiation of two African mouse species of genus *Mus* (Rodentia, Muridae). – *Rus. J. Genetics* 34: 80-85.
- Capanna, E. (1985): Karyotype variability and chromosome translocation in rodents: the case of the genus *Mus*. – pp. 643-669 in: *Evolutionary relationships among rodents* (eds. Luckett, W.P. & J.L. Hartenberger). – Plenum Publishing Corporation.
- Carpaneto, G.M. & S. Gippoliti (1994): Primates of the Haremma Forest, Ethiopia. – *Primate Conserv.* 11: 12-15.
- Duplantier, J.M., L. Granjon & K. Ba (1997): Repartition biogéographique des petits rongeurs au Sénégal. – *J. Afr. Zool.* 111: 17-26.
- Hutterer, R. & D.W. Yalden (1990): Two new species of shrews from a relic forest in the Bale Mountains, Ethiopia. – pp. 63-72 in: *Vertebrates in the Tropics* (eds. Peters, G. & R. Hutterer). – Museum Alexander Koenig, Bonn.
- Kingdon, J. (1971): East African mammals. An atlas of evolution in Africa. Vol. 1. – Academic Press, London & New York.
- Lavrenchenko, L.A., A.N. Milishnikov, V.M. Aniskin, A.A. Warshavsky & W. Gebrekidan (1997): The genetic diversity of small mammals of the Bale Mountains, Ethiopia. – *Sinet: Ethiop. J. Sci.* 20: 215-235.

- Lavrenchenko, L.A., W.N. Verheyen & J. Hulselmans (1998): Systematic and distributional notes on the *Lophuromys flavopunctatus* Thomas, 1888 species-complex in Ethiopia (Muridae - Rodentia). – Bull. Inst. Roy. Sci. Nat. Belg., Biologie 68: 199-214.
- Lavrenchenko, L.A., A.N. Milishnikov & A.A. Warshavsky (2000): The allozymic phylogeny: evidence for coherent adaptive patterns of speciation in Ethiopian endemic rodents from an isolated montane massif. – pp. 245-254 in: Isolated vertebrate communities in the tropics (ed. Rheinwald, G.). – Bonn. zool. Monogr. 46.
- Lisanework Nigatu & Mesfin Tadesse (1989): An ecological study of the vegetation of the Harennna Forest, Bale, Ethiopia. – Sinet: Ethiop. J. Sci. 12: 63-93.
- Rahbek, C. (1997): The relationships among area, elevation, and regional species richness in neotropical birds. – Am. Nat. 149: 875-902.
- Rohlf, F.J. (1988): NTSYS-pc: Numerical taxonomy and multivariate analysis system. Ver. 1.40. – Exeter Publishers, New York.
- Stevens, G.C. (1992): The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. – Am. Nat. 140: 893-911.
- Yalden, D. (1988a): Small mammals of the Bale Mountains, Ethiopia. – Afr. J. Ecol. 26: 281-294.
- Yalden, D. (1988b): Small mammals in the Harennna Forest, Bale Mountains National Park. – Sinet: Ethiop. J. Sci. 11: 41-53.
- Yalden, D.W., M.J. Lagen, D. Kock & J.C. Hillman (1996): Catalogue of the mammals of Ethiopia and Eritrea. 7. Revised checklist, zoogeography and conservation. – Tropical Zool. 9: 73-164.

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Ecology of *Otomys barbouri* Lawrence & Loveridge, 1953 (Mammalia, Rodentia): an endemic of the Afro-alpine zone of Mt Elgon, East Africa

Viola Clausnitzer

Abstract: The ecology of *Otomys barbouri* was studied on Mt Elgon, Uganda at an elevation of about 3700 m a.s.l. between October 1996 and November 1997 and additionally in March 1999. *Otomys barbouri* reached its highest population densities (22 ind./ha; equal to a biomass of about 2200 g/ha) in herbaceous and structured grasslands. The diet was entirely vegetarian, consisting mainly of grasses, different flowers (*Senecio*, *Helichrysum*, *Kniphofia*), and some herbs. Population dynamics and diet were studied in relation to climate and plant phenology; *Otomys barbouri* is non-seasonal. The microhabitat use and diets of *Otomys barbouri* and the sympatric *O. typus* are analysed and discussed in respect to fire succession in the Afro-alpine environment.

On Mt Elgon *O. barbouri* dominates in structured and species-rich grasslands, while *O. typus* mainly inhabits the pure tussock grasslands; both species avoid *Erica* and *Stoebe* stands. However, such ericaceous forest would cover large areas of Mt Elgon without fire, representing an unfavourable environment. The most important habitats for *Otomys*, the grassland communities, are the results of various fire histories. The homogenous tussock grasslands, dominated by *Festuca pilgeri*, indicate a very high fire frequency.

Key words: Afroalpine zone, fire ecology, rodents, population ecology, microhabitat use, Uganda

Introduction

“The mountains are Africa’s Galápagos Islands” (Kingdon 1989). The flora and fauna of these montane islands differ from the surrounding lowlands, since they harbour a number of endemics and species with highly disjunct distributions, as well as a number of unique life-forms. Some of these conspicuous elements can be found on virtually all of the East African mountains. Although montane forests formed a migration corridor in the last ice age, no evidence for continuous Afroalpine environments has been found so far (Hamilton 1982).

The isolated mountains of East Africa have never attracted the same degree of scientific attention as their neighbouring savanna biomes. Few studies on the Afroalpine rodent communities have been carried out, e.g. in the Simien Mts., focusing on the population ecology of *Arvicanthis blicki* (Müller 1977). This report will concentrate on two montane species of the Groove-toothed rat (*Otomys*). Species belonging to the genus *Otomys* were widespread and common in grassland biomes in Africa during the Plio-Pleistocene (Denys & Jaeger 1986, Denys 1989). Fossils of the whole subfamily Otomyinae predominate in southern African Pleistocene deposits (Bronner et al. 1988). The present distribution of *Otomys* is



Fig.1: Microscopic view of cell fragments from a faecal sample of *Otomys typus*. The larger cell compartments, with long, nearly rectangular cells, are *Festuca pilgeri*.

disjunct, mainly restricted to montane habitats in tropical Africa and to South African grasslands. These distribution patterns seem to be the results of climatic changes and competition with Murinae, which invaded Africa in the early Pliocene (Denys & Jaeger 1986, Denys 1989).

Otomys barbouri is endemic to the Afroalpine zone of Mt Elgon. This species was described by Lawrence & Loveridge (1953), was later considered to be a subspecies of *O. anchietae* and only recently was restored to species status again (Dieterlen & van der Straeten 1992). *O. typus* has a disjunct distribution on various East African mountains, and is most often restricted to elevations above 2000 m.

Study site

Mt Elgon (4321 m a.s.l.) is an isolated massif of volcanic origin straddling the Kenya/Uganda border (0°54'–1°25'N and 34°14'–34°45'E), which was deglaciated about 12 000 years BP. The volcano rises from a plateau 1850–2000 m high in the east and 1050–1350 m in the west; the longest north-south distance is about 80 km, the longest east-west distance 50 km.

The study sites were situated on the western slopes of Mt Elgon, between 3650 and 3800 m, near the Dirigana Valley. During the study period the precipitation at that elevation was 911 mm/y, April and September were the wettest months, the average temperature was 5.4° C.



Fig.2: Male *Otomys typus* with a transmitter round its neck (only the antenna is seen) for a radio-tracking study.

Methods

Three one-hectare grids were laid out for a mark-recapture study. Each of these grids consisted of 11 parallel lines, with 10 m spacing. The lines had trapping stations with two traps every 10 m, resulting in 121 trapping stations and 242 traps per grid. Trapping was done with Sherman live traps (Large and Extra Large) baited with a peanut-cassava flour mixture for four days each month from October 1996 to November 1997. Since both *Otomys* species were not attracted by any bait the traps were placed directly in their surface runway system. The difficulties of catching *Otomys* have been described before by various authors (e.g. Kingdon 1974, Shore & Garbett 1991).

The animals were individually marked by toe-clipping, weighed to the nearest gram, measured, and the sexual condition and ectoparasites were recorded.

The vegetation was mapped for all three grids, and the vertical structure measured using the point-intercept method; all plants were identified by Wesche (Wesche, in prep.).

Faeces of individuals were collected from the traps and later analysed using a microscope. For identification of the cell fragments in the pellets a cell catalogue was prepared from sampled plant species. Some of the cell fragments could be identified even to species level (fig.1).

Individuals of *Otomys typus* and *O. barbouri* were radio-tracked for several days (fig.2), using a TRX-10002 receiver (Wildlife Materials, Canada) and MD-2C transmitters (Holohil Systems, Canada).

Along a transect on the western slope of Mt Elgon sampling was done for two consecutive nights every two months (Oct. 1996–Oct. 1997) in different habitats between 2900 m and 4300 m. The traps were placed in three trap-lines (N–S direction) with 40 m spacing. Trap points were set at 20-m intervals, one small and one large break-back trap baited with peanut-cassava flour mixture were placed at each trap point. Additionally, five localities were trapped in the same pattern only once. In 4200 trap-nights, 384 rodents (13 species) were caught. The voucher specimens from this study are deposited in the Staatliches Museum für Naturkunde, Schloß Rosenstein, Stuttgart, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn and the Zoology Museum of the Makerere University, Kampala.

Rodents inhabiting the Afroalpine zone

A clear turnover of the vertical species composition on Mt Elgon occurs at about 3200 m a.s.l., which coincidences with the present upper limit of the montane forest (fig.3).

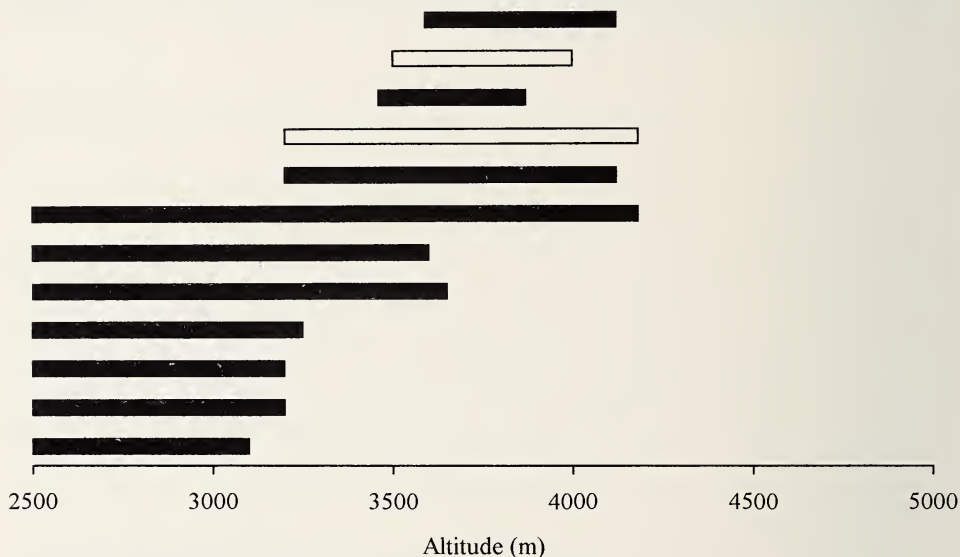


Fig.3: Vertical distribution of rodents on the western slopes of Mt Elgon; white bars indicate endemics.

Endemic rodents are only found in the Afroalpine zone, where they inhabit ericaceous vegetation, moorlands and tussock grasslands ranging between 3300 and 4300 m. The moorlands and tussock-grasslands above 3700 m on Mt Elgon are permanently inhabited by 9 rodent species, 8 of them belonging to the Muridae (table 1).

Table 1: Rodents found on Mt Elgon above 3700 m a.s.l.; the commonest ones are in bold.

Species	Author	Abundant in grassland habitats
Muridae		
<i>Cricetomys gambianus</i>	Waterhouse, 1840	
<i>Dendromys mesomelas</i>	(Brants, 1827)	X
<i>Grammomys dolichurus</i>	(Smuts, 1832)	
<i>Lophuromys flavopunctatus</i>	Thomas, 1888	X
<i>Otomys barbouri</i>	Lawrence & Loveridge, 1953	X
<i>Otomys typus</i>	Heuglin, 1877	X
<i>Rhabdomys pumilio</i>	(Sparrman, 1784)	X
<i>Tachyoryctes ruddi</i>	Thomas, 1909	X
Myoxidae		
<i>Graphiurus murinus</i>	(Desmarest, 1822)	

Population ecology

Otomys typus and *Otomys barbouri* are the commonest rodents in the Afroalpine zone of Mt Elgon. They have been recorded at densities of 32 (*O. typus*) and 23 (*O. barbouri*) individuals per hectare, giving a biomass of 3200 and 2200 g per ha respectively.

A total number of 87 *Otomys barbouri* and 177 *O. typus* were marked individually on the three grids. The recapture rates of all marked specimens were 67% for *O. barbouri* and 72% for *O. typus*. In the second half of the study, of the total monthly capture at least 80% were recaptured.

The home-range sizes for both species did not vary between males and females; the given estimates were calculated using the 100% convex polygon method (fig.4).

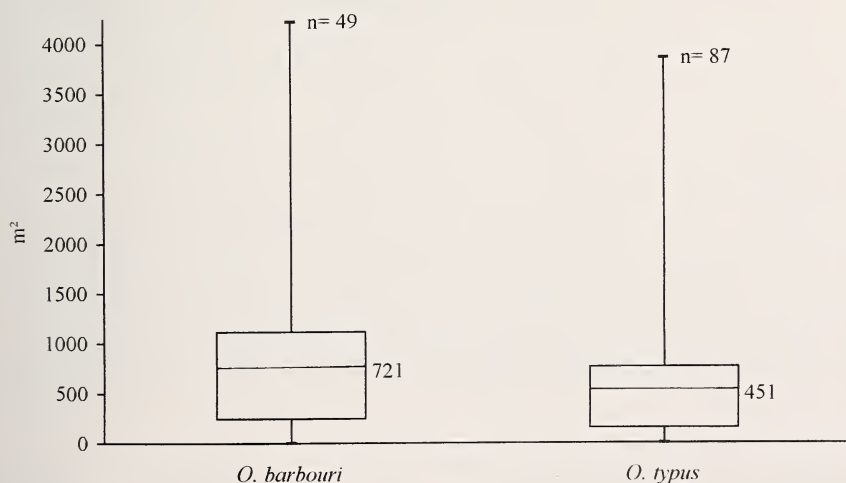


Fig.4: Home-range sizes for *Otomys barbouri* and *O. typus* based on a one-year mark-recapture study at about 3700 m on Mt Elgon; 100% convex polygons.

The population size estimates for the different grids, calculated by the “minimum number alive” method, did not fluctuate much and not in parallel patterns between the plots over the year. There was no correlation between climatic conditions and population fluctuations. Both species showed no seasonality, reproduction occurred throughout the year. The weight gain of individual males underlines this statement (fig.5).

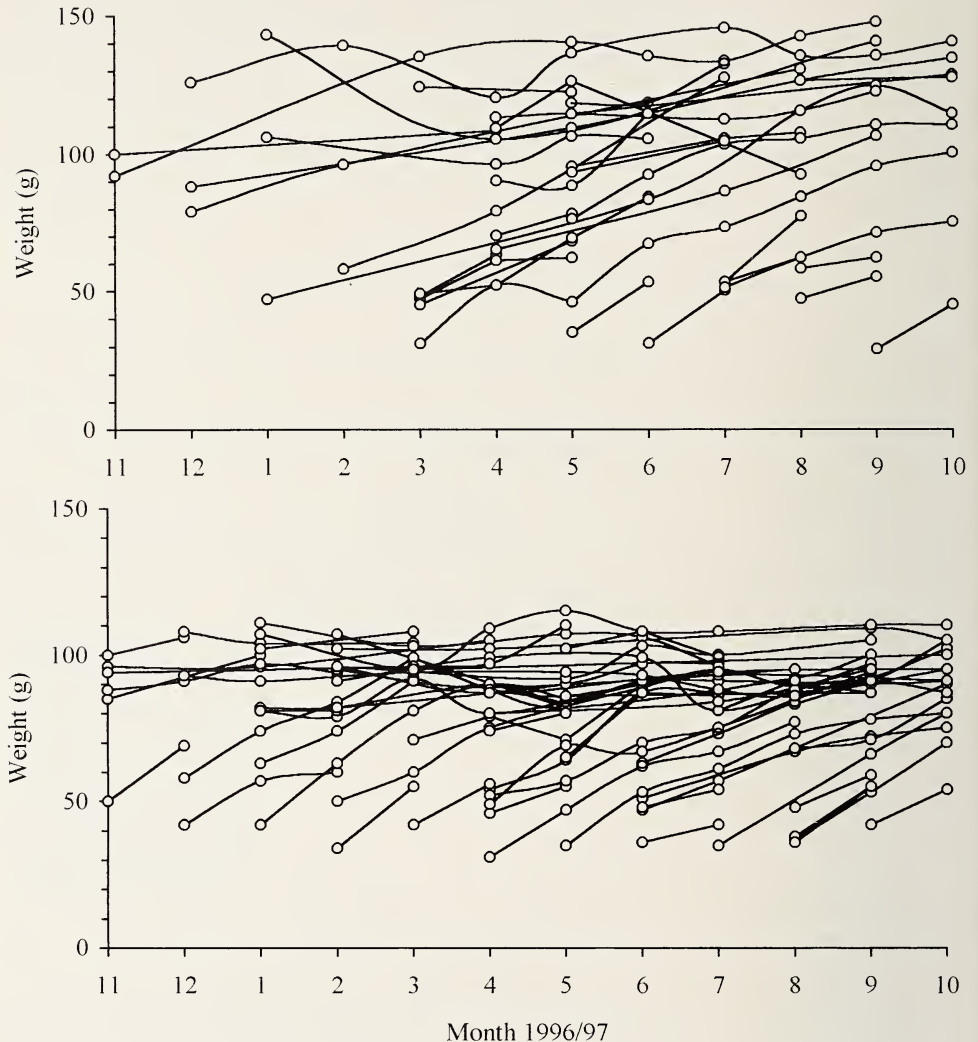


Fig.5: Weight gain or loss in individual males of *Otomys barbouri* (top) and *O. typus* (bottom); Mt Elgon, 3600–3800 m.

Although one might think that the climatic conditions in the Afroalpine zone have a strong influence on the rodents, *Otomys barbouri* and *O. typus* did not show any seasonality. Reproduction, population fluctuations, or weight gain/loss did not

correlate with climatic variations. Both species reproduce the whole year round and no evidence for unfavourable seasons could be found.

Diet composition

The faecal analyses showed no significant fluctuation in diet composition over the year (fig.6). The diet of *Otomys typus* consisted mainly of grasses, of which *Festuca pilgeri* (fig.1) made up 50%. In the pellets of *Otomys barbouri* all grasses together totalled only about 50%, the other cell fragments being from dicotyledons, mainly parts of Compositae inflorescences.

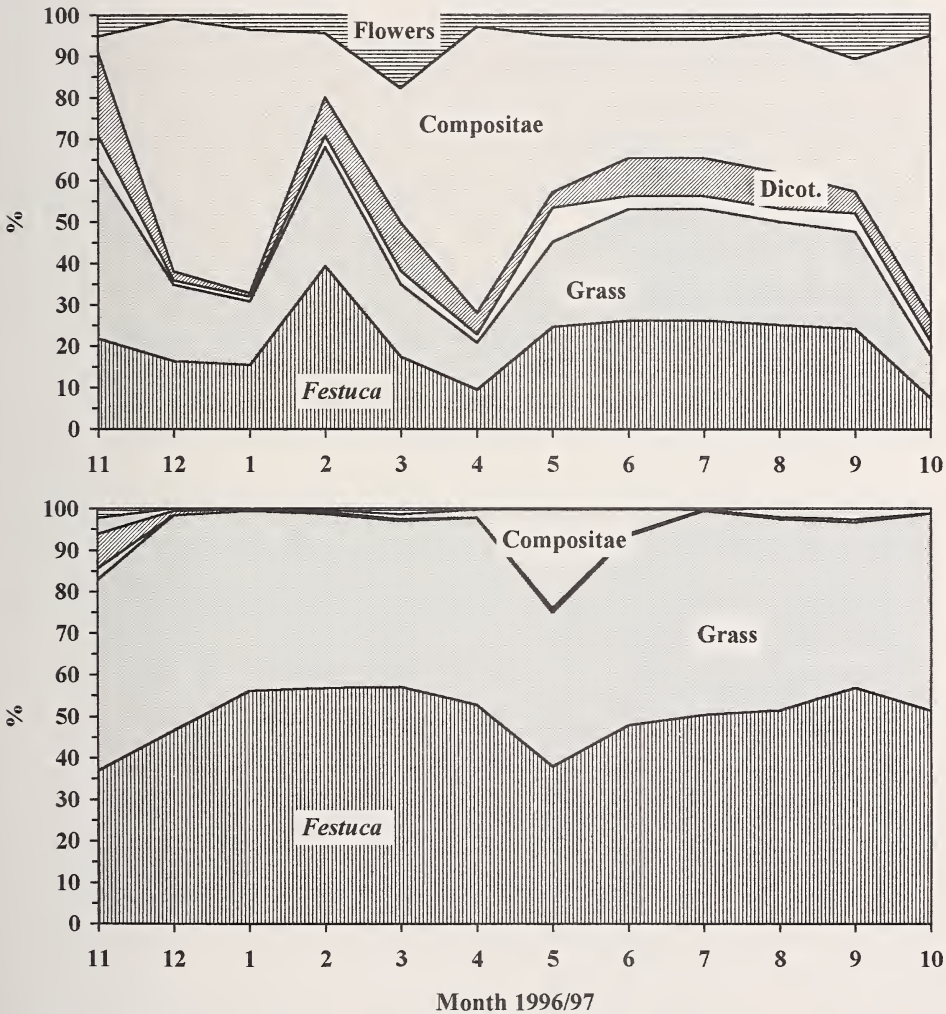


Fig.6: Faecal analyses, based on monthly collected pellets on Mt Elgon for *Otomys barbouri* (top) and *O. typus* (bottom).

The genus *Otomys* is a highly adapted herbivore, relying exclusively on grasses and herbs (Perrin & Curtis 1980). The two species studied on Mt Elgon were strictly herbivorous: *Otomys typus* feeding mainly on grasses, *O. barbouri* on grasses and dicotyledons. Food, especially grasses, is not a limiting factor for the species on Mt Elgon. The phenology of the plants is not markedly seasonal (Wesche in prep.) and flowers, a preferred food of *Otomys barbouri*, are available throughout the year.

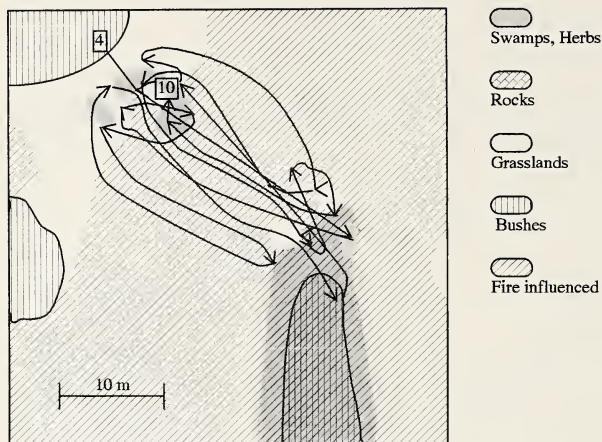


Fig.7: Daily movements of a male of *Otomys barbouri* (4.-10.Mar.1999). Arrows indicate the morning, noon and evening fixes, starting on the morning of the 4th; Mt Elgon, 3600 m.

Movements

The radio-track study gave an impression of the daily ranges of the animals, although the maximum time one individual could be followed up was 9 days. All radio-tracked individuals (n=15) moved a total maximum distance of 35 m, most often moving to and fro between the same areas (fig.7). Both species occurred in the same areas, but used different microhabitats (fig.8), the range used being very restricted over the observed days.

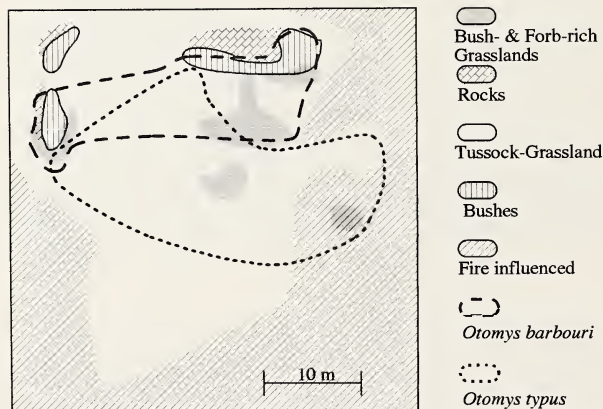


Fig.8: Ranges of a male *Otomys barbouri* and a male *O. typus* (28.Feb.-5.Mar. 1999); Mt Elgon

Although being very unsociable, which is the case in most *Otomys* species (e.g. Davis 1972, Dieterlen 1968, Vermeulen & Nel 1988), the animals do not establish territories, the home-ranges of both species and different sexes overlapping strongly. If animals meet in the field, they give a warning noise and normally each moves away. Fights were not observed in the study. Additionally, no evidence for fights, like cut ears or tails, were found.

Microhabitat use

Both *Otomys* species coexist sympatrically in large areas on Mt Elgon, but they show significant differences in their microhabitat use (fig.9). The local distribution of each species depends on vegetation composition and structure and plant species richness. The differences in distribution of *Otomys barbouri* on structured and species-rich grasslands and of *O. typus* on *Festuca pilgeri* dominated tussock grasslands was significant (χ^2 -test: $n = 53$, $p = 0.018$).

Fig.9 compares the abundance (trap grids) of the Elgon endemic *Otomys barbouri* with the more widely distributed *Otomys typus*. Black squares indicate the position

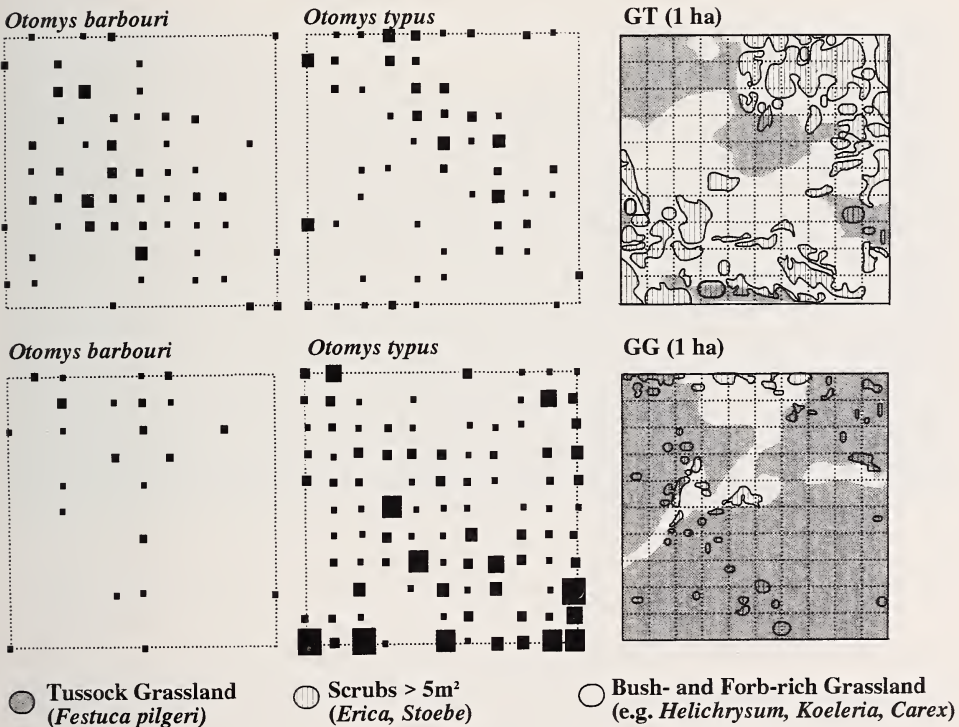


Fig.9: Comparison of two trap grids, upper line at 3650 m a.s.l., lower line at 3750 m. Left squares indicate the position of traps within the grids, black squares symbolize numbers of individuals of the given species caught in a trap. Data for a full year summarized. Drawings on the right indicate the corresponding vegetation structure.

of traps within the grid where animals were caught, sizes of the squares symbolize the numbers of individuals. The sketch map of the vegetation in the grids allows an assessment of the pattern. *Otomys barbouri* prefers patchy grasslands or those rich in shrubs, whereas pure tussocks are avoided. In contrast, *O. typus* avoids patchy vegetation and prefers tussock grasslands. Dense scrub is inhabited by neither of the species. The lower grid is a much more uniform grassland. In consequence the endemic species is rare, whereas *Otomys typus* is abundant. The comparatively small home-ranges (fig.4) make such microhabitat analysis possible.

Fig.10 gives an example of the two preferred habitats of *Otomys* on Mt Elgon. Radio-tracked *Otomys typus* (n=4) moved only within the *Festuca pilgeri* grassland shown in the foreground. Individuals of *O. barbouri* (n=3) spent most of their time in the *Helichrysum* and *Dendrosenecio* bush seen in the background.



Fig.10: Habitats of *Otomys*; *O. typus* is mainly found in the *Festuca pilgeri* grasslands shown in the foreground, *O. barbouri* in the *Helichrysum* and *Dendrosenecio* thicket behind; Mt Elgon, 3600 m.

Fire as an important factor in landscape formation

The present distribution of the different grassland formations in the Afroalpine zone of Mt Elgon, which I have discussed as the important habitats for *Otomys*, is a result of a long history of fire. The importance of fires in Afroalpine ecosystems is well known and was described in detail by Hedberg (1964). Mt Elgon is mentioned as having been particularly affected by man (Hedberg 1951, Beck et al. 1987). The impact of fire on the ericaceous and grassland communities on Mt Elgon were directly observed (Wesche et al. in press). Fires, which are all man-made, appear to be the major agent in replacing the natural ericaceous vegetation

with grassland communities. Without fires the upper ericaceous belt up to about 4000 m on Mt Elgon would naturally consist of dwarf *Erica* forest, with more open and shrubby communities only in bogs or on shallow rocky soils. Megaherbivores, like Elephant and Buffalo probably had a large impact on the vegetation, leaving open areas of different successions and sizes. Today relics of unburned ericaceous vegetation mainly survive in fire-safe rocky sites.

Both *Otomys* species profit from the fire-induced change towards dominating grasslands. *Otomys barbouri* prefers vegetation mosaics such as those created by rare fires. With increasing fire frequency the vegetation is converted into pure tussock grasslands, which are avoided by *O. barbouri*, but inhabited in high densities by *O. typus*. An example for this situation is given in the lower drawing of fig.8. Without any fire, both species would be very limited in their distribution, with scattered occurrences in naturally open or patchy vegetation in a dense ericaceous forest.

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References

- Beck, E., H. Rehder, E.D. Schulze & J.O. Kokwaro (1987): Alpine Plant Communities of Mt- Elgon.- An Altitudinal Transect Along the Koitoboss Route. – J. East Afr. Nat. Hist. Soc. and Nat. Mus.76: 1-12.
- Bronner, B., S. Gordon & J. Meester (1988): *Otomys irroratus*. – Mammalian Species 308: 1-6.
- Davis, R.M. (1972): Behaviour of the Vlei Rat, *Otomys irroratus* (Brants, 1827). – Zool. Afr. 7: 119-140.
- Denys, C. (1989): Phylogenetic affinities of the oldest East African *Otomys* (Rodentia, Mammalia) from Olduvai Bed I (Pleistocene, Tanzania). – N. Jb. Geol. Paläont. Mh. 44: 705-725.
- Denys, C. & J.J. Jaeger (1986): A biostratigraphic problem: The case of the East African plio-pleistocene rodent faunas. – Modern Geol.10: 215-233.
- Dieterlen, F. (1968): Zur Kenntnis der Gattung *Otomys* (Otomyinae; Muridae; Rodentia). Beiträge zur Systematik, Ökologie und Biologie zentralafrikanischer Formen. – Z. Säugetierk. 33: 321-352.
- Dieterlen, F. & E. van der Straeten (1992): Species of the genus *Otomys* from Cameroon and Nigeria and their relationship to East African forms. – Bonn. zool. Beitr. 43: 383-392.
- Hamilton, A.C. (1982): Environmental History of East Africa – A Study of the Quaternary. – Academic Press, London.
- Hedberg, O. (1951): Vegetation belts of the east-african mountains. – Svensk Bot. Tidskr. 45: 141-196.
- Hedberg, O. (1964): Features of afroalpine plant ecology. – Almqvist & Wiksells Boktryckeri, Uppsala.

- Kingdon, J. (1974): East African Mammals – Hares and Rodents. – Academic Press, London.
- Kingdon, J. (1989): Island Africa. – Princetown University Press, Princetown.
- Lawrence, B. & A. Loveridge (1953): Zoological results of a 5th Expedition to East Africa. I: Mammals from Nasaland and Tete; with a note on the genus *Otomys*. – Bull. Mus. Comp. Zool. Harvard 110.
- Müller, J.P. (1977): Populationsökologie von *Arvicanthis abyssinicus* in der Grassteppe des Semien Mountains National Park (Äthiopien). – Z. Säugetierk. 42: 145-172.
- Perrin, M.R. & B.A. Curtis (1980): Comparative morphology of the digestive system of 19 species of Southern African myomorph rodents in relation to diet and evolution. – South Afr. J. Zool. 15: 22-33.
- Shore, R.F. & S.D. Garbett (1991): Notes on the small mammals of the Shira Plateau, Mt. Kilimanjaro. – Mammalia 55: 601-607.
- Vermeulen, H.C. & J.A.J. Nel (1988): The bush Karoo rat *Otomys unisculatus* on the Cape West coast. – South Afr. J. Zool. 23: 103-111.
- Wesche, K. (in prep.): Ecology of the high-altitude environment on Mt. Elgon (Uganda/Kenya). Vegetation and climatic conditions. – Ph.D. thesis, Univ. of Marburg.
- Wesche, K., V. Clausnitzer, S. Miede & G. Miede (in press): Habitat conditions in afroalpine communities – examples from East Africa. – Proc. 1st Symp. “AFW Schimper-Stiftung”.

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Allozymic phylogeny: evidence for coherent adaptive patterns of speciation in Ethiopian endemic rodents from an isolated montane massif

L.A. Lavrenchenko, A.N. Milishnikov & A.A. Warshavsky

Abstract: Genetic relationships within the two presumably monophyletic species groups, *Lophuromys flavopunctatus* species complex and *Praomys albipes* - *Stenocephalemys* spp. assemblage, which demonstrate clear patterns of elevational replacement in the Bale Mountains, were studied using a starch-gel electrophoretic analysis of 17 loci. Data were analyzed by both phenetic and cladistic procedures, considering both allele and loci as characters. The revealed phylogenetic patterns in two independently evolving endemic assemblages showed a high level of concordance. The species of the Afroalpine zone (*L. melanonyx* and *S. albicaudata*) belong to ancestral lineages. The low-altitude populations of the heathland species (*L. brevicaudus* and *S. griseicauda*) group with the forest species (*L. chrysopus* and *P. albipes* respectively) from the same altitudes. These clusters appear as sister groups to populations of *L. brevicaudus* and *S. griseicauda* from higher altitudes. Our results indicate an early origin of the Afroalpine rodent fauna and recent descent of the Ethiopian forest rodent fauna. We speculate that *L. chrysopus* and *P. albipes* descended from still extant parental taxa (*L. brevicaudus* and *S. griseicauda* respectively) by "explosive" adaptive evolution.

Key words: *Lophuromys*, *Stenocephalemys*, *Praomys*, Ethiopia, allozymes, phylogeny, evolution

Introduction

The diverse and unique Ethiopian small mammal fauna demonstrates clear patterns of an altitudinal zonation, including some examples of elevational replacement of congeners (Rupp 1980, Yalden 1988). Three endemic species belonging to the *Lophuromys flavopunctatus* species complex, *L. chrysopus*, *L. brevicaudus* and *L. melanonyx*, occur in the Bale Mountains, replacing each other in the different altitudinal belts (tropical forest - heathland - Afroalpine zone) with very little overlap (Lavrenchenko et al. 1998). This altitudinal distribution closely matches the distributional pattern of another presumably monophyletic group of closely related endemic murides, including *Praomys albipes*, *Stenocephalemys griseicauda* and *S. albicaudata*, which inhabit the same vegetation zones respectively in the Bale Mountains (Yalden 1988). The habitat segregation occurring among these closely related taxa suggests an adaptive pattern of speciation. The present study used allozyme data to reconstruct the phylogenies of these two presumably monophyletic assemblages.

Material and methods

Sampling. Field work was carried out in the course of the Joint Ethio-Russian Biological Expedition (JERBE) between January and April 1995. Specimens were collected at the following localities in the Bale Mountains National Park (fig.1):

(1) *Podocarpus* belt of the Harenna Forest (1780 m a.s.l., 6°31'N, 39°44'E) - 2 *L. chrysopus*, 3 *P. albipes*;

(2) *Aningeria* belt of the Harenna Forest (1935 m a.s.l., 6°38'N, 39°44'E) - 2 *L. chrysopus*, 3 *P. albipes*;

(3) *Schefflera-Hagenia* belt of the Harenna Forest in the Katcha area (2400 m a.s.l., 6°42'N, 39°44'E) - 8 *L. chrysopus*, 2 *L. brevicaudus*, 13 *P. albipes*, 1 *S. griseicauda*;

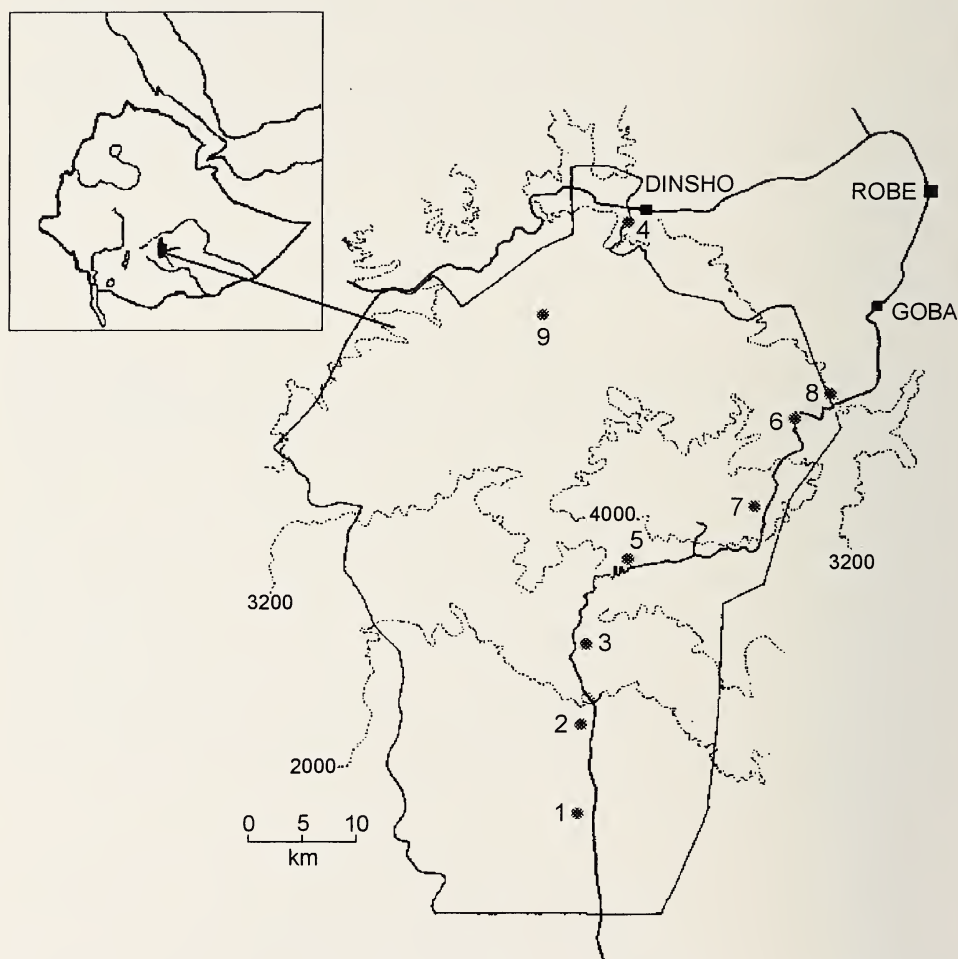


Fig.1: Map of the Bale Mountains National Park, showing trapping sites. See text for abbreviations of localities.

- (4) Mosaic grassland/forest habitats in the Dinsho area (3170 m a.s.l., 7°06'N, 39°47'E) - 33 *L. brevicaudus*, 2 *P. albipes*, 5 *S. griseicauda*;
- (5) Ericaceous belt of southern slope of the Sanetti Plateau (3700 m a.s.l., 6°46'N, 39°46'E) - 3 *S. albocaudata*;
- (6) Ericaceous belt of northern slope of the Sanetti Plateau (3750 m a.s.l., 6°54'N, 39°55'E) - 2 *L. brevicaudus*;
- (7) Afroalpine belt with sparse and short vegetation in Konteh area of the Sanetti Plateau (4050 m a.s.l., 6°51'N, 39°53'E) - 21 *L. melanonyx*, 6 *S. albocaudata*;
- (8) Ericaceous belt in Chorchora area (3500 m a.s.l., 6°56'N, 39°56'E) - 19 *L. brevicaudus*, 1 *S. griseicauda*, 2 *S. albocaudata*;
- (9) Swamp shore areas in Kotera (3500 m a.s.l., 7°00'N, 39°41'E) - 15 *L. brevicaudus*, 3 *L. melanonyx*, 1 *S. griseicauda*, 3 *S. albocaudata*.

Electrophoretic analysis of proteins. Standard horizontal starch-gel electrophoresis and staining techniques, as described by Selander et al. (1971) and Harris & Hopkinson (1978), were performed to analyze genic variation in 17 enzymatic and non-enzymatic proteins. The enzymatic proteins (their respective abbreviations and Enzyme Commission Numbers are given in parentheses) were alcohol dehydrogenase (ADH; 1.1.1.1); diaphorase (DIA-1, DIA-2; 1.6.2.2); glucose-6-phosphate dehydrogenase (G-6PD; 1.1.1.49); glutamate-oxaloacetate transaminase (GOT; 2.6.1.1); glycerophosphate dehydrogenase (GPD; 1.1.1.8); isocitrate dehydrogenase (IDH; 1.1.1.42); lactate dehydrogenase (LDH-A, LDH-B; 1.1.1.27); malate dehydrogenase (MDH-1, MDH-2; 1.1.1.37); malic enzyme (ME-1; 1.1.1.40); sorbitol dehydrogenase (SDH; 1.1.1.14); superoxide dismutase (SOD-1, SOD-2; 1.15.1.1). The non-enzymatic proteins were haemoglobin (HBB) and albumin (ALB).

Phylogenetic analysis. The conspecific samples of *L. chrysopus* and *P. albipes* from adjacent localities 1, 2 and 3, and *S. albocaudata* from localities 5 and 7 were pooled basing on the analyses of homogeneity. The genetic divergence among populations and species were evaluated by Nei's (1978) and Rogers's (1972) genetic distances. Phylogenetic trees were computed from genetic distances using the Fitch-Margoliash least squares method (FM trees), neighbor-joining method (NJ trees) (PHYLP v.3.5c (Felsenstein 1993)) and distance-Wagner procedure (DW trees) as employed in the BIOSYS-1 package (Swofford and Selander 1989).

Cladistic analysis was performed using both loci and alleles as characters. In the former case we treated the most common allele as the character state and utilized Fitch parsimony criteria; both Wagner and Dollo parsimony criteria were applied in the latter case (PHYLP v.3.5c). Bootstrap analyses involving at least 500 replications were conducted to assess the reliability of the branching patterns of FM and parsimony trees. *Mus cf. triton*, *M. mahomet* and two cryptic *Otomys* species from the Bale Mountains (for details, see Lavrenchenko et al. 1997) were used as outgroups in the phylogenetic analyses of the *Praomys albipes* - *Stenocephalemys* spp. assemblage and the *Lophuromys flavopunctatus* species complex respectively.

Results

Marked intraspecific genetic differentiation in *L. breviceaudus*, *S. griseicauda*, and *S. albocaudata* was revealed. The values of Nei's unbiased genetic distance between some samples of these species (table 1, 2) are above those normally encountered for conspecific populations ($D < 0.105$; Thorpe 1983). The genetic distances between *L. breviceaudus* from locality 6 and all other "*breviceaudus*" populations fall within the value usually recorded for interspecific genetic differentiation in rodents. The mean genetic distance between the sample of *L. breviceaudus* from locality 9 and three remaining conspecific populations was $D = 0.110$, which corresponds to the genetic differentiation of rodent allopatric species.

Table 1: Values of Nei's genetic identity (above the diagonal) and genetic distance (below the diagonal) between *Lophuromys* populations.

L.b. = *L. breviceaudus*; L.c. = *L. chrysopus*; L.m. = *L. melanonyx*; Ot.56 = *Otomys* (2n=56); Ot.58 = *Otomys* (2n=58).

Population	1	2	3	4	5	6	7	8	9	10
1 L. b. 4	*****	0.828	0.968	0.885	0.995	0.804	0.791	0.743	0.216	0.252
2 L. b. 6	0.188	*****	0.823	0.745	0.861	0.689	0.682	0.661	0.241	0.230
3 L. b. 8	0.032	0.194	*****	0.908	0.957	0.763	0.750	0.779	0.214	0.251
4 L. b. 9	0.123	0.295	0.096	*****	0.894	0.676	0.778	0.830	0.211	0.246
5 L. b. 3	0.005	0.150	0.044	0.112	*****	0.803	0.821	0.752	0.225	0.263
6 L. c. 1,2,3	0.218	0.372	0.270	0.392	0.219	*****	0.593	0.531	0.245	0.187
7 L. m. 7	0.235	0.383	0.288	0.251	0.198	0.523	*****	0.948	0.296	0.318
8 L. m. 9	0.298	0.414	0.250	0.187	0.285	0.634	0.054	*****	0.282	0.311
9 Ot. 56	1.535	1.423	1.540	1.557	1.492	1.405	1.219	1.267	*****	0.790
10 Ot. 58	1.377	1.469	1.383	1.401	1.336	1.678	1.146	1.168	0.236	*****

Table 2: Values of Nei's genetic identity (above the diagonal) and genetic distance (below the diagonal) between *Stenocephalemys* and *Praomys albipes* populations.

P.a. = *P. albipes*; S.g. = *S. griseicauda*; S.a. = *S. albocaudata*; M.m. = *M. mahomet*; M.t. = *Mus cf. triton*.

Population	1	2	3	4	5	6	7	8	9	10	11
1 P. a. 1,2,3	*****	0.999	0.889	0.940	0.654	0.733	0.665	0.708	0.533	0.065	0.119
2 P. a. 4	0.001	*****	0.881	0.940	0.642	0.723	0.653	0.696	0.520	0.060	0.119
3 S. g. 4	0.118	0.126	*****	0.944	0.783	0.864	0.750	0.785	0.613	0.061	0.121
4 S. g. 3	0.062	0.061	0.057	*****	0.706	0.788	0.718	0.760	0.588	0.060	0.118
5 S. g. 9	0.425	0.443	0.244	0.348	*****	0.970	0.718	0.790	0.689	0.060	0.118
6 S. g. 8	0.311	0.324	0.146	0.238	0.030	*****	0.709	0.784	0.679	0.061	0.121
7 S. a. 5,7	0.408	0.426	0.288	0.331	0.331	0.343	*****	0.827	0.620	0.114	0.120
8 S. a. 9	0.345	0.363	0.242	0.274	0.236	0.244	0.190	*****	0.714	0.121	0.119
9 S. a. 8	0.630	0.655	0.489	0.531	0.373	0.387	0.477	0.337	*****	0.123	0.182
10 M. t. 3	2.734	2.806	2.789	2.821	2.821	2.791	2.168	2.115	2.095	*****	0.417
11 M. m. 4	2.130	2.125	2.108	2.140	2.140	2.110	2.123	2.127	1.701	0.875	*****

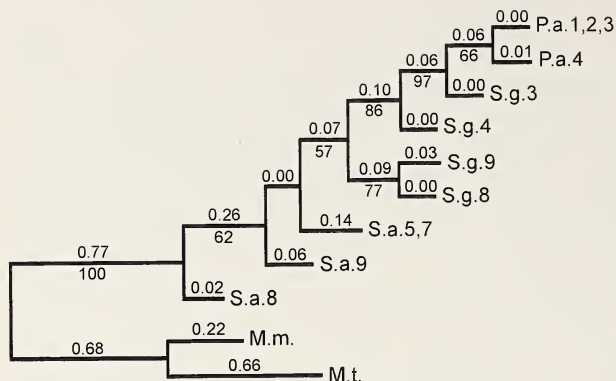


Fig.3: Fitch-Margoliash tree computed from Nei's genetic distances between *Stenoccephalemys* and *Praomys albipes* populations. Numbers above a line are distances; below, the bootstrap values. The tree is rooted at the composite outgroup. For abbreviations of populations see table 2.

(1) the species of the Afroalpine zone (*L. melanonyx* and *S. albocaudata*) occupy basal positions in the phylogenies;

(2) the youngest lineages are represented by the forest species (*L. chrysopus* and *P. albipes*);

(3) the heathland species (*L. brevicaudus* and *S. griseicauda*) may be paraphyletic. Indeed, there are preliminary indications that our samples of *S. griseicauda* include more than one species (Lavrenchenko et al. 1997). A discussion on this point will be published elsewhere. By contrast, our cytogenetic (Aniskin et al. 1997) and morphological (Lavrenchenko et al. 1998) analyses support the conspecificity of all our samples of *L. brevicaudus*. Therefore we carried out parsimony analyses at the species level with populations being pooled together. The results of the two analyses treating both loci and alleles as characters were fully compatible with those based on the distance data. *L. melanonyx* diverges basally whereas *L. chrysopus* and *L. brevicaudus* are sister groups. The high bootstrap values indicate significant support for this branching pattern (fig.4).

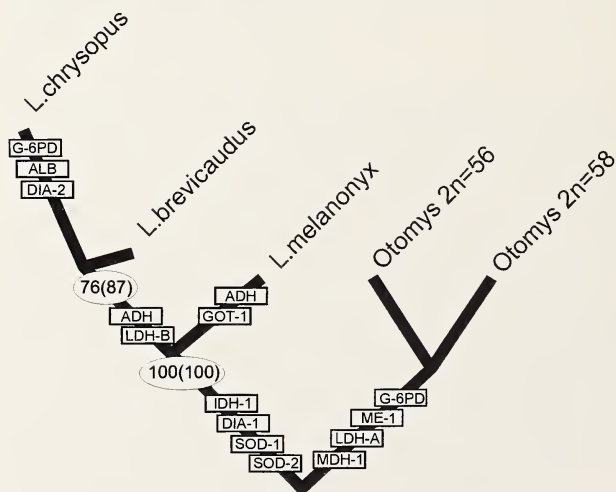


Fig.4: The most parsimonious tree resulting from cladistic analyses of *Lophuromys* species. Branch lengths are drawn proportionately to those resulting from the analysis by locus using Fitch parsimony. Synapomorphies for the analysis by locus (changes of the most common allele in a locus) are indicated along the branches. Circled numbers are bootstrap values for the analyses by locus and by allele, the latter given in parentheses).

Discussion

The most surprising result of our phylogenetic analyses – which, we believe, is not an artifact of sampling – is the association of low-altitude populations of the heathland species (*L. brevicaudus* and *S. griseicauda*) with the forest species (*L. chrysopus* and *P. albipes* respectively) from the same altitudes, so that the clusters thus formed appear to be sister groups to populations of the heathland species from higher altitudes. There are three possible theoretical explanations of this phenomenon: (1) possible limited hybridization between sympatric populations of the related species; (2) a high level of homoplasy (parallelism) in allozymic variation caused by climatic factors obscuring true patterns of relationships; (3) the explosive nature of speciation of the forest species.

The first possibility seems unlikely in view of the lack of individuals heterozygous at a number of diagnostic loci, and chromosomal characteristics (Lavrenchenko et al. 1997) of both species assemblages from narrow overlap zones. Although the second possibility is difficult to exclude completely, we note that the allozyme expression patterns demonstrate no clear pattern of correlation with geoclimatic variables both in forest and heathland species. As far as the *Stenocephalemys* complex is concerned, the difference between the two groups of populations of *S. griseicauda* is too high (table 2) to be accounted for by a local adaptive shift of allele frequencies. Therefore, the hypothesis postulating “explosive” evolution of *L. chrysopus* and *P. albipes*, both having descended from still extant parental taxons (*L. brevicaudus* and *S. griseicauda* respectively) seems to be favourable. It is worth mentioning that these forest species are the most divergent forms in their species assemblages with respect to chromosomal characteristics (Lavrenchenko et al. 1997). In addition, *P. albipes* was so divergent morphologically from *Stenocephalemys* spp. that it was even attributed to another genus. These evidences suppose an accelerated rate of chromosomal and morphological evolution under speciation of *P. albipes* and of chromosomal and genetic evolution of *L. chrysopus*. The morphological differentiation may be at least partly explained by adaptations to a forest environment. It has been suggested (Nevo 1985) that chromosomal repatterning may facilitate adaptive evolution (e.g. by providing new superior supergenes for ecotypic adaptation). In general, evolution of the two forest taxa may be interpreted within the framework of the invasive model of chromosomal speciation (White 1982). The recent origin of the endemic *L. chrysopus* and *P. albipes* from aboriginal lineages suggests that the Ethiopian forest rodent fauna has no direct relation to those of Central Africa. The resemblance of these two Ethiopian taxa to “true” forest species of *Lophuromys* and *Praomys* from the rest of Africa may be a result of convergent evolution.

The concordant phylogenetic patterns within two independently evolving endemic assemblages provide evidence of similar speciation histories and can be related to significant climatic and environmental changes during the Pliocene-Pleistocene. We presume that differentiation of the immediate ancestors of the two groups studied (probably similar morphologically to *L. brevicaudus* and *S. griseicauda*) occurred during the late Pliocene (2.4 Mya), when heathland had become established on the Ethiopian plateaux (Yalden &

Largen 1992). The specialized *L. melanonyx* and *S. albocaudata* adapted to the high altitudes apparently represent Lower Pleistocene splits connected with the formation of Afroalpine habitat. The recent origin of *L. chrysopus* and *P. albipes* may be associated with some humid period of the Pleistocene, when the treeline in the mountains was rising. It is worth mentioning that in the Bale Massif, in Pleistocene times, a significant area was covered by glaciers; their terminal moraines are at 3100 -3200 m a.s.l. (Messerli & Winiger 1980). A spatial fragmentation having resulted from such conditions may have facilitated the speciation events. On the other hand, an isolation of local populations by glaciers during some periods of the Pleistocene may explain the very high level of interpopulational genetic differentiation in *L. brevicaudus*, *S. griseicauda* and *S. albocaudata* and their possible paraphyly.

We can conclude that sharp altitudinal zonation, extremely diverse geomorphology, drastic environmental changes in the past, and the isolated position of the Bale Massif has made this unique area a real center of diversification and endemism for Ethiopian rodents. To clarify in more detail the interrelationships among these species, further analysis taking into consideration, an extended set of allozyme loci or other genetic data is warranted.

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References

- Aniskin, V.M., L.A. Lavrenchenko, A.A. Varshavskii & A.N. Milishnikov (1997): Karyotypic differentiation of three harsh-furred mouse species of genus *Lophuromys* (Murinae, Rodentia) from the Bale Mountains National Park, Ethiopia. – Russ. J. Genetics 33: 818-824.
- Felsenstein, J. (1993): PHYLIP Phylogeny Inference Package, ver. 3.5c. – University of Washington.
- Harris, H. & D.A. Hopkinson (1978): Handbook of enzyme electrophoresis in human genetics. – North-Holland Publ. Comp., Amsterdam; Amer. Elsevier Publ. Comp., New York.
- Lavrenchenko L.A., W.N. Verheyen & J. Hulselmans (1998): Systematic and distributional notes on the *Lophuromys flavopunctatus* Thomas, 1888 species-complex in Ethiopia (Muridae – Rodentia). – Bull. Inst. Roy. Sci. Nat. Belg. (Biol.) 68: 199-214.
- Lavrenchenko, L.A., A. N. Milishnikov, V.M. Aniskin, A.A. Warshavsky & W. Gebrekidan (1997): The genetic diversity of small mammals of the Bale Mountains, Ethiopia. – Sinet: Ethiop. J. Sci. 20: 213-233.

- Messerli, B. & M. Winiger (1980): The Saharan and East African upland during the Quaternary. – pp.87-118 in: The Sahara and the Nile (eds. Williams, M.A.J. & H. Faure). – Balkema, Rotterdam.
- Nei, M. (1978): Estimation of average heterozygosity and genetic distance from a small number of individuals. – *Genetics* 89: 583-590.
- Nevo, E. (1985): Speciation in action and adaptation in subterranean mole rats: patterns and theory. – *Boll. Zool.* 52: 65-95.
- Rogers, J.S. (1972): Measures of genetic similarity and genetic distance. – *Stud. Genet.* 7. Univ. Texas Publ. 7213: 145-153.
- Rupp, H. (1980): Beiträge zur Systematik, Verbreitung und Ökologie äthiopischer Nagetiere: Ergebnisse mehrerer Forschungsreisen. – *Säugetierkd. Mitt.* 28: 81-123.
- Selander, R.K., M.H. Smith, S.Y. Yang, W.E. Johnson & J.B. Gentry (1971): Biochemical polymorphism and systematics in the genus *Peromyscus*. 1. Variation in the old-field mouse (*Peromyscus polinotus*). – *Stud. Genet.* 6. Univ. Texas Publ. 7103: 49-90.
- Swofford, D.L. & R.B. Selander (1989): BIOSYS-1: a computer program for the analysis of allelic variation in population genetics and biochemical systematics. Release 1.7. – Illinois Natural History Survey, Champaign.
- Thorpe, J.P. (1983): Enzyme variation, genetic distance and evolutionary divergence in relation to levels of taxonomic separation. – pp.131-152 in: Protein Polymorphism: Adaptive and Taxonomic Significance (eds. Oxford, G.S. & D. Rollinson). – Academic Press, London.
- White, M.J.D. (1982): Rectangularity, speciation and chromosome architecture. – pp. 75-102 in: Mechanisms of Speciation (ed. Barigozzi, C.). – Alan R. Liss, New York.
- Yalden, D. (1988): Small mammals of the Bale Mountains, Ethiopia. – *Afr. J. Ecol.* 26: 281-294.
- Yalden, D.W. & M.J. Largen (1992): The endemic mammals of Ethiopia – *Mamm.Rev.* 22: 115-150.

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Primates in Eritrea – distribution and habitat

D. Zinner, F. Torkler & F. Peláez

Abstract: Eritrea, the former northern part of Ethiopia, is one of the youngest countries in the world since it became independent from Ethiopia in 1993. Due to several decades of civil war, information on status and distribution of wildlife and birds in Eritrea is outdated and incomplete. A stock-taking program of biological resources and biodiversity is one of the aims of the Eritrean government. We assisted in the program by doing a survey on primate (*Papio hamadryas*, *Papio anubis* and *Cercopithecus a. aethiops*) distribution and abundance in eastern and central Eritrea. Information obtained during the study will be integrated in a national wildlife management and conservation plan in Eritrea.

We interviewed local people using a questionnaire to gather information about baboon (*Papio* sp.) and Grivet (= Vervet) monkey (*Cercopithecus a. aethiops*) sleeping sites, and about predator and wildlife presence. The sleeping sites were then visited to the nearest possible point and their position was recorded using a GPS. We took notes on the surrounding vegetation and the nearest watercourse. We also categorized vegetation at around 100 selected sites, independently of the primate sites, as reference points for a subsequent classification of Landsat MSS satellite data. We included the geographical position of sleeping sites, other evidence of baboons and monkeys, and information on the vegetation in a subsequent GIS analysis and mapping. Habitats were described by altitude, precipitation, and vegetation cover and plant productivity.

In our survey area, we found 78 sleeping cliffs of Hamadryas baboons, 8 sites with Olive baboons and 43 sites with Grivet monkeys. A clear geographical separation between the two *Papio* species became obvious, whereas Grivet monkeys are sympatric with both baboon species. In contrast to other wildlife, the current distribution of baboons and monkeys seems not to deviate from their historical distribution and the proposed national parks will include several of the primate sites.

Key words: Eritrea, *Papio hamadryas*, *Papio anubis*, *Cercopithecus a. aethiops*, distribution, ecology

Introduction

The central highlands of Ethiopia and Eritrea were refuge areas for plant and animal species during glacial times and have had a very profound effect upon the evolution, composition and distribution of the flora and fauna of NE Africa. Here we can find a unique assemblage of montane species, including many endemics. In the surrounding drier lowlands, a mixture of species of different zoogeographic regions meet: species of the East African savannas, of the sub-Saharan savanna belt, of the North African deserts and the Somali arid zone. Even species belonging to the Palaearctic Region are present in the area (Yalden et al. 1996). The number of mammalian taxa recorded from Ethiopia has been rising steadily during the past 30 years, as a result of both taxonomic revisions and new discoveries. Yalden et al. (1996) recognized 277 terrestrial and 11 marine species, but state that these numbers are still provisional.

Most of the biogeographic work of recent decades in Ethiopia was confined to the politically more stable central parts of the country, so information on species status in the northern areas is outdated and incomplete. In 1991, after a 30-year-long struggle for independence, the northern part of Ethiopia, the former Italian colony Eritrea, became an independent state. Presently the Ministry of Agriculture and the Department of Environment of Eritrea are preparing a National Biodiversity Strategy and Action Plan, but most of the relevant information on species distribution and abundance is missing. Actually for most of the taxa information was never collected or derives from sources older than 50 years.

To overcome this serious data deficiency, the Ministry of Agriculture started a series of wildlife surveys. We focused on primates and gathered information about their distribution and abundance in central and eastern Eritrea, particularly Hamadryas baboons. Additionally, we were interested in the gross ecological condition of primate habitats and their variation by ecological zone and species. Information obtained during our study will be integrated in a national wildlife management and conservation plan in Eritrea.

Eritrea

Eritrea is located in NE Africa on the coast of the Red Sea with an area of 120,000 km². It holds an estimated human population of 3.5 million. Eritrea encompasses several ecological zones which differ in altitude and distance from the Red Sea, and thus in annual rainfall and plant productivity.

From east to west we find the coastal lowlands that stretch up to 40 km inland, with their south-eastern extension, Dankelia, an inhospitable, volcanic area with low rainfall and very high temperatures. The lowlands are followed by a sudden rise within 40 km up to 3000 m, the eastern escarpment. Next come the central highlands and the Hamasien plateau, including the catchment areas of the Anseba and Mareb rivers, the main area of settlement and agriculture. The terrain in the western escarpment drops steeply down again from 2200 m to 1000 m into the western lowlands, which extend in the west to the Sudanese border, there reaching an altitude of 500 m.

Primate species

There are historical reports of the occurrence of six primate species in Eritrea: *Galago* sp., *Colobus guereza*, *Cercopithecus a. aethiops*, *Theropithecus gelada*, *Papio anubis* and *Papio hamadryas*. The presence of *Colobus* is very doubtful, because there is almost no adequate habitat in Eritrea, and *Galago* and *Theropithecus* were not confirmed (Yalden et al. 1977).

Method

Survey

We conducted our survey during October–November 1997 and March–April 1998 and October 1998. The survey covered more than 25 000 km² (16°19' to 14°17'N, 37°13' to 39°53'E) with an additional extension to the west up to the Sudanese border (36°16'E) to include the Olive baboon (*Papio anubis*) region. We

interviewed local administrators and people in villages using a questionnaire to gather information about baboon (*Papio* sp.) and Grivet (*Cercopithecus a. aethiops*) sleeping sites, predator and wildlife presence. The people are normally very well informed about baboons and grivets in their neighbourhood, because in most areas baboons and monkeys are recognized as a threat to crops and gardens. We visited the sleeping sites of the baboons and monkeys to the nearest possible point and recorded their position and altitude by GPS. Whenever possible we tried to estimate the number of primates using the sleeping site and we took notes on the surrounding vegetation for a subsequent food analysis, and the nearest watercourse. Additionally, we recorded all other sites where we found evidence of primates.

Primate habitats in Eritrea

In our ecological description of primate habitats in Eritrea, we used the following parameters.

- Precipitation: data on annual precipitation (mm y^{-1}) derive from the National Map of Eritrea 1:1,000,000 and from meteorological stations of the Ministry of Agriculture.
- Altitude: the altitude and position of sleeping sites and other points of interest was directly determined by GPS. Average altitude of home-ranges and maximum elevational difference in home-ranges were calculated from an elevation model of Eritrea (pixel size: $0.9 \times 0.9 \text{ km}$) to the nearest 100 m (U.S. Geological survey 1997).

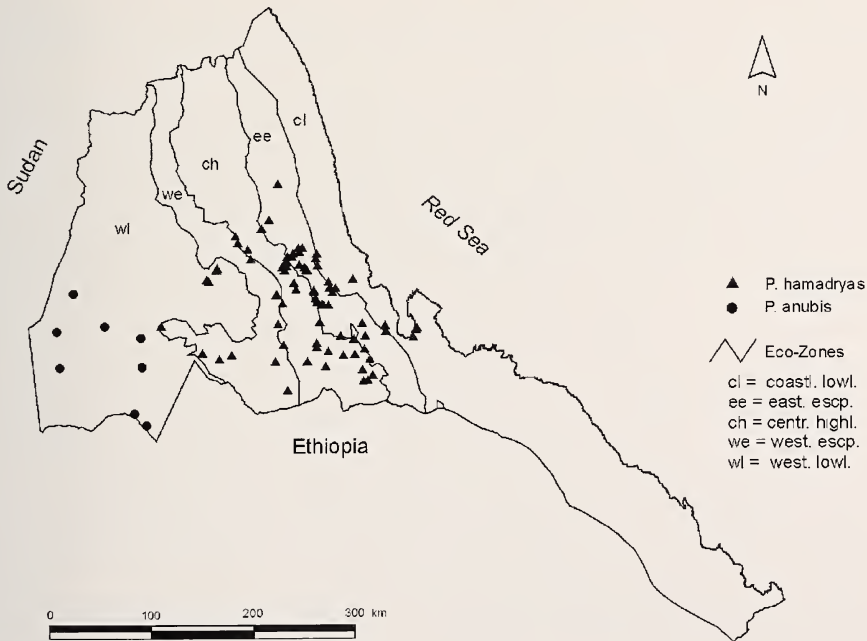


Fig.1: Distribution of Hamadryas and Olive baboons (*Papio hamadryas*, *Papio anubis*) in central Eritrea.

– Normalized Difference Vegetation Index (NDVI): the NDVI is a measure of the amount and vigor of vegetation at the surface. The magnitude of NDVI is related to the level of photosynthetic activity in the vegetation. In general, higher values of NDVI indicate greater vigor and amounts of vegetation. Thus areas with higher NDVI normally have a higher plant productivity. Pixel size after rectification was 7.6 x 7.9 km. We used 10 years of dekadal data, starting in 1982, to calculate the average NDVI for each pixel of the terrestrial area Eritrea (U.S. Geological Survey 1997).

– Vegetation classification: a vegetation classification of the survey area was carried out. We used the White (1983) classification for African environments with additional categories which seem to be important for baboons. Apart from the sites where we encountered primates, we categorized vegetation at around 100 selected sites as reference points for a subsequent classification of Landsat MSS satellite data (Zinner & Torkler 1996). Our classification corresponds reliably with official data from the Ministry of Agriculture.

GIS analysis

For an ecological description of primate habitats we encircled each baboon site with a buffer of 3 km radius, thus producing a 28.3 km² area as a hypothetical

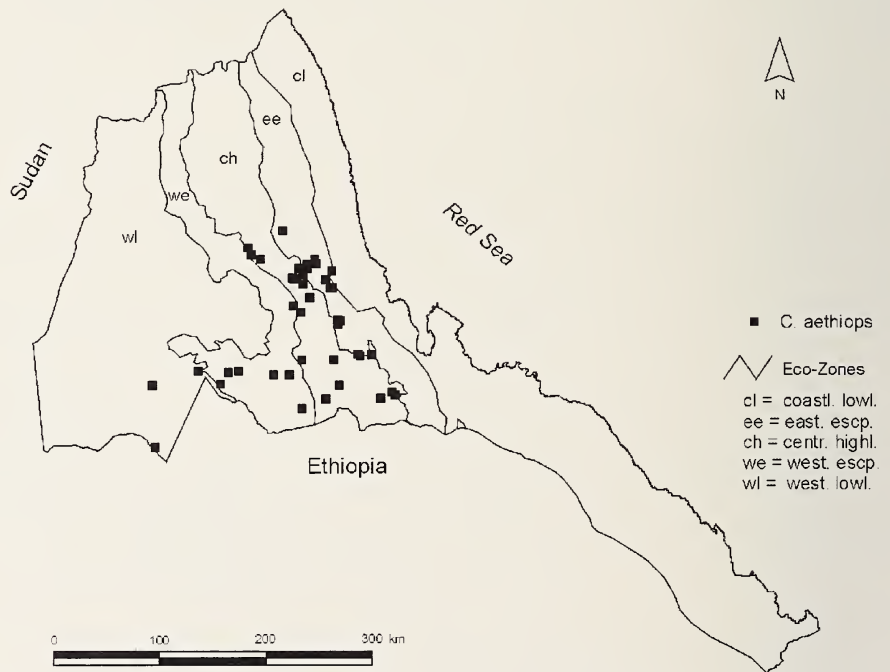


Fig.2: Distribution of Grivet monkeys (*Cercopithecus a. aethiops*) in central Eritrea

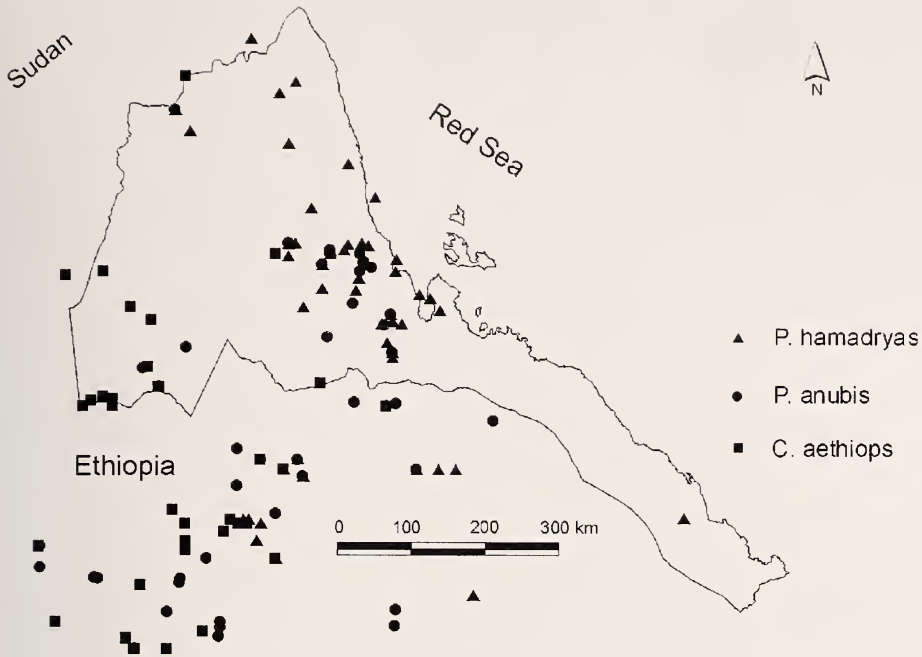


Fig.3: Historical distribution of *Papio hamadryas*, *Papio anubis* and *Cercopithecus aethiops aethiops* in northern Ethiopia and Eritrea (Yalden et al. 1977).

home-range of the group. Similarly, grivet sites were provided with a 0.5 km radius buffer. These home-range sizes correspond with data from other baboon and grivet studies (Cheney 1987). We included the geographical position of primate sites and information on the vegetation in a subsequent GIS analysis and mapping. Primate habitats were then described by their ecological parameters. We compared the habitats of the three species and primate habitats in the five different eco-zones.

Results

We found 78 sleeping cliffs of *Papio hamadryas* at all altitudes of all ecological zones, from the coastal area to the western lowland (fig. 1). In 49 cases, we were able to estimate the number of individuals that congregate at the sleeping cliff. In the south-western part of the western lowlands, Olive baboons replace Hamadryas baboons. Here we encountered 8 small groups of Olive baboons (6–28 individuals).

We detected Grivet monkeys at 43 different sites in all ecological zones except the coastal lowlands (fig.2). Hamadryas and Olive baboons have exclusive ranges, whereas Grivet monkeys are sympatric with both baboon species. Overall, the current distribution of *Papio hamadryas* and *Papio anubis* seems not to deviate from their historical distribution as reported by Yalden et al. (1977) (fig.3).

The precipitation and elevation data of primate home-ranges in Eritrea are given in table 1. Hamadryas baboons live in areas with less than 200 mm up to 1000 mm precipitation.

Table 1: Ecological parameters of *Papio hamadryas* (*P.ham.*), *Papio anubis* (*P.anu.*) and *Cercopithecus a. aethiops* (*C.aeth.*) home-ranges in the five ecological zones of Eritrea. Precipitation (mm y^{-1}), altitude of site (m), maximum elevational difference within home-ranges (m).

Eco-zone	species	n	precipitation (mm y^{-1})		altitude of record (m)		max. elevational difference in HR (m)	
			range	mean	range	mean	range	mean
coastal lowland	<i>P.ham.</i>	7	100–600	200	33–393	195	100–700	371
eastern escarpm.	<i>P.ham.</i>	24	100–1000	517	350–2300	1407	200–1400	858
central highland	<i>P.ham.</i>	30	400–900	557	1491–2736	2061	200–1200	627
western escarpm.	<i>P.ham.</i>	13	400–800	538	830–2268	1527	100–1000	523
western lowland	<i>P.ham.</i>	4	350–400	388	656–750 ^c	697	300–400	350
coastal lowland	<i>C.aeth.</i>	0	–	–	–	–	–	–
eastern escarpm.	<i>C.aeth.</i>	11	400–1000	641	850–2064	1493	0–500	182
central highland	<i>C.aeth.</i>	20	400–600	508	1511–2575	2028	0–600	150
western escarpm.	<i>C.aeth.</i>	9	400–800	578	975–2049	1543	0–400	100
western lowland	<i>C.aeth.</i>	3	700–800	750	788–1030	876	0–100	33
western lowland	<i>P.anu.</i>	8	400–800	580	601–853	760	100–300	200

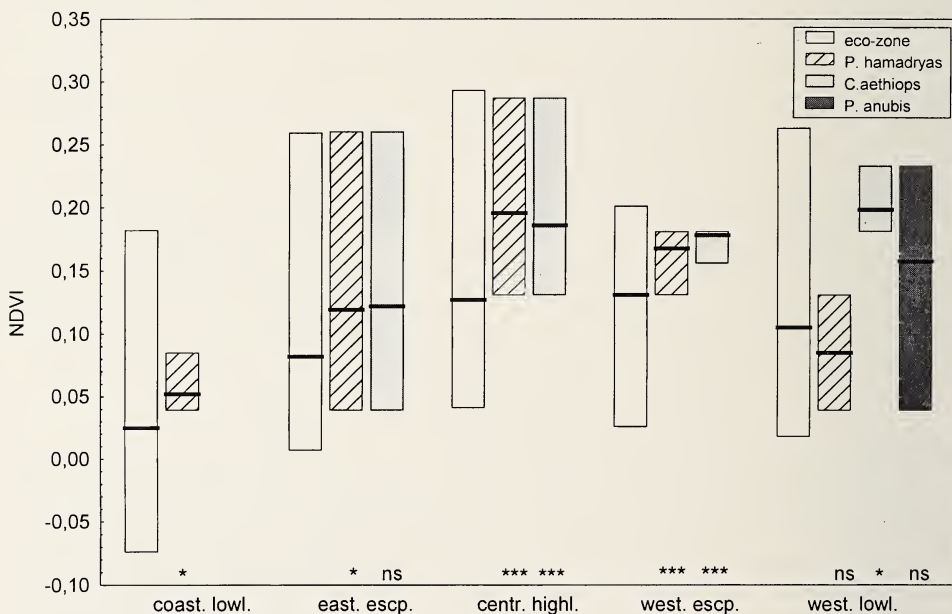


Fig.4: Normalized Difference Vegetation Indices (NDVI) of Eritrean eco-zones and of *Papio hamadryas*, *Papio anubis* and *Cercopithecus a. aethiops* home-ranges (means and ranges, single mean test; *Papio hamadryas*: coastal lowland $n=7$, eastern escarpment $n=24$, central highlands $n=30$, western escarpment $n=13$, western lowland $n=4$; *Papio anubis*: western lowland $n=8$; *Cercopithecus a. aethiops*: eastern escarpment $n=11$, central highlands $n=20$, western escarpment $n=9$; western lowland $n=3$. NDVI classes: -0.162 to -0.029 = very poor vegetation, middle; -0.028 to 0.105 = very poor vegetation, high; 0.106 to 0.155 = poor vegetation, low; 0.156 to 0.205 = poor vegetation, high; 0.206 to 0.259 = middle vegetation, low; 0.260 to 0.313 = middle vegetation, high).

Interestingly, in the western lowlands we detected them in the drier areas, whereas Grivets and Olive baboons live in more humid areas. Hamadryas baboons were found from sea level up to almost 3000 m. At the western border of their distribution, they occupy altitudes above 650 m. Olive baboons live in areas below the 900 m contour line. Grivets occupy similar altitude as the baboons. In the mountainous areas, the maximum elevation difference within Hamadryas home-ranges can reach up to 1400 m. In some of their home-ranges these baboons have to surmount these elevation difference on a daily basis, when they go down to the water source and up again to their sleeping cliff.

The mean Normalized Difference Vegetation Indices (NDVI) for primate home-ranges in comparison with NDVIs of eco-zones are given in Fig. 4. Eritrea has only poor NDVIs, with the poorest condition in the coastal lowlands. In most eco-zones, primate home-ranges have an NDVI significantly higher than the respective eco-zone mean. Hamadryas baboons seem to be the most tolerant species. Their mean NDVIs for the coastal and western lowlands are the lowest of all primate home-ranges. A comparison of species reveals that in the eastern escarpment, the central highlands and the western escarpment Hamadryas baboons and Grivet monkeys use areas with similar mean NDVIs. In the western lowlands, however, the discrepancy between Hamadryas baboons and Olive baboons and Grivet monkeys becomes

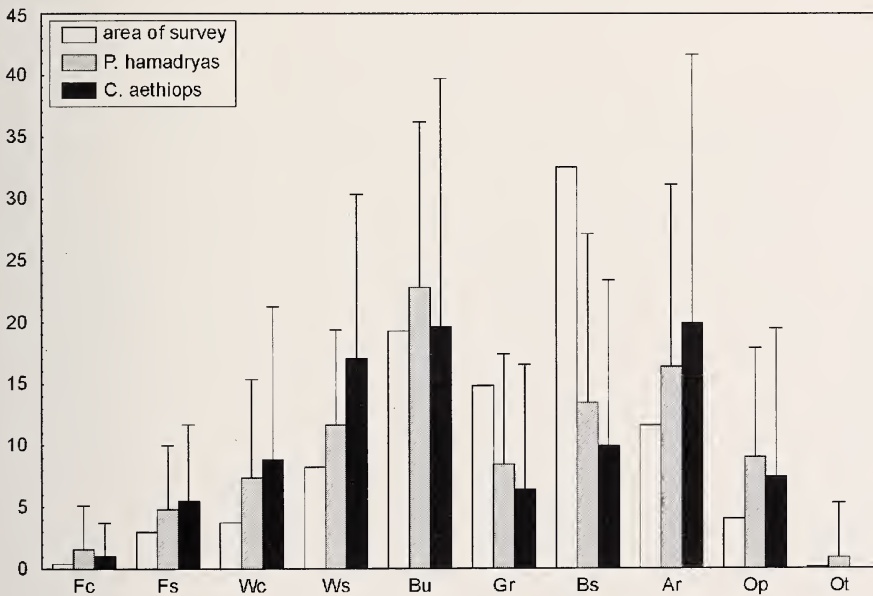


Fig.5: Proportion of vegetation and ground-cover classes in Eritrea (area of survey) and in home-ranges of *Papio hamadryas* and *Cercopithecus a. aethiops*. Area surveyed: 34087 km²; *P. hamadryas* n=68, 1923 km²; *C. aethiops* n=35, 27 km². Fc = closed/medium-closed forest; Fs = open forest; Wc = closed/medium-closed woodland; Ws = open woodland; Bu = bush-/shrubland; Gr = grassland/wooded grassland; Bs = barren soil; Ar = agriculture; Op = *Opuntia* spp.; Ot = other (settlements, rivers, lakes).

obvious. On average, Olive baboons and Grivet monkeys occur in areas with higher NDVIs than Hamadryas baboons (*P. anubis*: $t=2.06$, $p=0.0659$; *C. aethiops*: $t=4.27$, $p=0.0079$). No difference was found between mean NDVIs of Grivet monkey areas and Olive baboon areas.

The result of the vegetation classification of the eastern parts of our study area are given in fig.5. On average, the vegetation in Hamadryas baboon home-ranges was 2 % closed or medium-closed forest, 5 % open forest, 8 % closed woodland, 12 % open woodland, 23 % bush and shrubland, 8 % grassland and wooded grassland, 14 % barren soil and rocks, 16 % agriculture and 9 % prickly pear stands (*Opuntia ficus-indica*). Others, such as settlements and inland waters, represented less than 0.1 %. We could not classify 3 % of the satellite images because of cloud and shadow. A similar picture emerged for the grivet home-ranges, with one exception. In their home-ranges, open woodland was significantly more frequent than in baboon home-ranges. If we compare the overall vegetation distribution in our area of survey with the vegetation in primate home-ranges, it becomes obvious that both species select more wooded areas and reject the very open areas like grassland and barren soil.

The number of Hamadryas baboons encountered at sleeping cliffs varied from 25 to 800, with a mean of 190. From this figure, we estimate a population of at least 15 000 Hamadryas baboons in our survey area.

Discussion

During a five-month survey, we gathered information on distribution and abundance of primates in central and eastern Eritrea, particularly on Hamadryas baboons. We detected Hamadryas baboons in all five ecological zones and Olive baboons only in the south-western part of the western lowland. Grivet monkeys are sympatric with both baboon species. A geographical separation of the two baboon species, and sympatry of *Cercopithecus aethiops* with *Papio anubis* was reported from Ethiopia by Dunbar & Dunbar (1974). An exception to the allopatry of the baboon species is an area of overlap that exists in central Ethiopia (Nagel 1973). So far we have not discovered such a zone in Eritrea, but there is probably an area west of Barentu where the ranges of the two species overlap. Ecologically, Hamadryas baboons seem to be the most tolerant species, occupying the widest range of habitats, from the marginal dry and hot coastal lowlands to the sub-humid and moist slopes and mountain tops of the eastern escarpment and the central highlands. Hamadryas baboons in Saudi Arabia and Yemen show a similar altitudinal distribution and ecological plasticity (Biquand et al. 1992, Al-Safadi 1994). Olive baboons are confined to the moist and low-lying areas in the south-west, with relatively high plant productivity. The likely borderline between the two species is the 700 to 900 m contourline in the western lowlands. Grivet monkeys share the habitat with both baboon species. Since they are much more arboreal than the baboons they are more restricted in their range to wooded areas. In most parts of our survey area we found grivets in river valleys, where they foraged in the riverine trees, particularly in large fig trees. They do not only search for their food in different parts of the habitat, but also feed on other parts of plants than the more

terrestrial baboons and competition is therefore reduced (Dunbar & Dunbar 1974). We can expect much more competition between the baboons because there is a broad overlap in diet and habitat use (Kummer 1968, Barton et al. 1993). It remains puzzling which factors hinder one or the other species in expanding its range, although, at least in some areas, the conditions seem to be suitable for both.

In most parts of Eritrea, monkeys and baboons are the only larger wildlife still remaining and they are recognized as a threat to crops and gardens. Hunting and killing of wild animals is illegal, nevertheless people chase primates out of their areas and sometimes kill them. With intensification of agricultural activities through irrigation projects, the conflict between primates and humans will become more intense. However, the Eritrean government is planning national parks that will also include primate habitats (EAE 1995).

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References

- Al-Safadi, M. (1994): The hamadryas baboon, *Papio hamadryas* (Linnaeus, 1758) in Yemen (Mammalia: Primates: Cercopithecidae). – Zool. Middle East 10: 5-16.
- Barton, R.A., A. Whiten, R.W. Byrne & M. English (1993): Chemical composition of baboon plant foods: implications for the interpretation of intra- and interspecific differences in diet. – Folia Primatol. 61: 1-20.
- Biquand, S., V. Biquand-Guyot, A. Boug & J.P. Gautier (1992): The distribution of *Papio hamadryas* in Saudi Arabia: Ecological correlates and human influence. – Int. J. Primatol. 13: 223-243.
- Cheney, D.L. (1987): Interactions and relationships between groups. – pp. 267-281 in: Primate Societies (eds. Smuts, B.B., D.L. Cheney, R.W. Seyfarth, R.W. Wrangham & T.T. Struhsaker). – The University of Chicago Press, Chicago.
- Dunbar, R.I.M. & E.P. Dunbar (1974): Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. – Folia Primatol. 21: 36-60.
- EAE Eritrean Agency for the Environment (1995): National Environmental Management Plan for Eritrea. – Government of Eritrea, Asmara, Eritrea.
- Kummer, H. (1968): Social organization of hamadryas baboons. A field study. – The University of Chicago Press, Chicago.
- Nagel, U. (1973): A comparison of anubis baboons, hamadryas baboons, and their hybrids at a species border in Ethiopia. – Folia Primatol. 19: 104-165.

- White, F. (1983): The Vegetation of Africa. – UNESCO.
- Yalden, D. W., M. J. Lagen, & D. Kock (1977): Catalogue of the mammals of Ethiopia. 3. Primates. – *Monitore Zool. Ital. (NS) Suppl.* 9: 1-52.
- Yalden, D. W., M. J. Lagen, D. Kock, & J. C. Hillman (1996): Catalogue of the mammals of Ethiopia and Eritrea. 7. Revised checklist, zoogeography and conservation. – *Tropical Zoology* 9: 73-164.
- Zinner, D. & F. Torkler (1996): GIS and remote sensing techniques as tools for surveying primates. – *Ecotropica* 2: 41-47.
- Maps and geographical data:
- National Map of Eritrea (1995): 1:1,000,000. – Government of Eritrea, Asmara, Eritrea.
- U.S. Geological Survey 1997: Edition: 1, Sioux Falls, SD, USA, EROS DataCenter / International Program.

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Effects of fragmentation and assessing minimum viable populations of lemurs in Madagascar

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Abstract: Lemur species assemblages on Madagascar show highly nested structures in forest fragments of different size. This allows us to predict with a high degree of probability which species will most likely go extinct if the available habitat decreases in size. We use this predictable pattern to identify the minimum viable populations of different lemur species that were able to survive for 20–40 years in forest fragments. According to this analysis, populations of about 40 adult individuals are able to survive for 20–40 years. Populations of this size require between 20 and 800 ha of suitable forest. Fragments of this size no longer exist in the littoral forests of the southeastern portion of the island and are rare in the western dry deciduous forests.

Key words: Madagascar, lemurs, fragmentation, nested subset, minimum viable populations

Introduction

Over the last few decades the forests of Madagascar have been reduced dramatically in extent (Green & Sussman 1990, Nelson & Horning 1993). The situation is precarious, in particular for the dry deciduous forests of western Madagascar (Smith 1997) and for the littoral forests along the east coast (Du Puy & Moat 1996). Apart from forest reduction in general, fragmentation of the remaining forests is severe and several species of lemur occur only in a few remaining forest fragments (e.g., *Propithecus tattersalli*, *P. diadema perrieri*, *Eulemur macaco flavifrons*, *Lepilemur dorsalis*; reviewed in Mittermeier et al. 1994).

In view of these developments, there are now several plans for reforestation in order to rehabilitate lost habitat for lemurs and other forest-dependent species (Holloway 1999). Reforestation can be used to extend and create buffer zones around natural forests, and to link remaining forest fragments that could then act as reservoirs from where native species could colonize the new habitats. In the domain of the western deciduous forest, secondary forests grow very slowly and do not provide suitable habitat for lemurs even after 40 years of regeneration (Sorg 1996, Ganzhorn & Schmid 1998), though mixed tree plantations can be used by lemurs after a few years (Ganzhorn & Abraham 1991). Under more favorable conditions in the domain of the eastern humid forests, tree plantations and native trees seem to grow fast enough to provide acceptable habitat for many (though not all) lemur species after a few years (Ganzhorn 1987, Goodman & Rakotondravony 1998).

While programs for reforestation and rehabilitation of fallow land progress in other parts of the world (e.g., Lamb 1998), there is little information available for Madagascar. Many reforestation projects on the island include patches of natural forest in their restoration strategy. These patches of forest should serve as sources from where species can colonize the regrowing habitat. One problem that we address here for Madagascar is the question of how big the patch of native forest has to be to allow the indigenous plant and animal species to survive in these forest fragments until the restored vegetation can provide suitable habitat for them to expand into.

Lemurs were chosen for this study because they are among the largest forest-dependent vertebrate species of Madagascar. We therefore consider them "umbrella species". If remaining forest patches are large enough to allow their survival, these fragments should also allow survival of many other forest-dependent species. To resolve this question we review the consequences of forest fragmentation in various regions of Madagascar to find out which extent of forest is required to allow a given lemur species to survive for the next 20–40 years (i.e., the time needed for establishing tree plantations).

Methods

We conducted a literature search to obtain information on lemurs occurring at several forest sites that had been fragmented some 20–40 years ago (table 1). This information was condensed into presence/absence data in these forest fragments. To assess the effect of fragmentation, the presence/absence data of lemurs in these fragments were compared to the composition of lemur communities in a nearby

Table 1: Summary of data used to assess the effects of forest fragmentation on lemurs

Study site	Domain and forest type	Range of fragment size [ha]	Large forest block for comparison	no. of fragments	Reference
Menabe	West; dry deciduous	0.6-600	Kirindy/CFPF	10	Ganzhorn et al. 1999b
Mahatsinjo	East; evergreen	240	Ankilahila	1	Goodman & Schütz 1999
Sahivo Antanamalaza	East; evergreen	100: 231	Betampona	2	Britt et al. 1999*
Tampolo	East; littoral, evergreen	675	Ambatovaky	1	Goodman & Rakotondravony 1998
Manafiafy, Mandena	South; littoral forest	20-457	Anosyennes, Vohimenas	9	Lewis Environmental Consultants 1992; own data

* only diurnal species

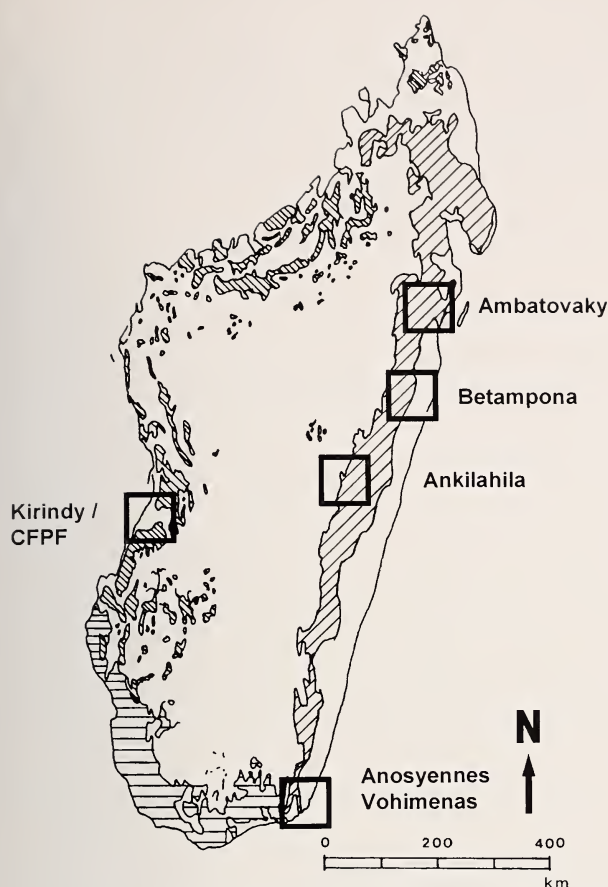


Fig. 1. Location of sites considered to assess the effect of fragmentation on lemur communities. Shaded areas mark forest: humid forests are in the east, dry deciduous forests are in the west and spiny forests are in the south

large block of forest that was assumed to contain the complete set of extant lemur species known from each of these regions. Data were also supplemented with results from ongoing studies in the littoral forests near Tolagnaro, in the extreme southeastern portion of the island (fig. 1).

Population size of the different lemur species in a given fragment at the time of isolation was estimated by multiplying fragment size with the average population density of the lemur species in relatively undisturbed forests (Ganzhorn et al. 1999a). We then plotted population size against fragment size to assess the transitions between fragments of differing size where a given lemur species occurs in one fragment but is absent in the next smaller fragment. We assume that the lemur species was also present in the smaller fragment at the time of isolation, but that a population of that size was too small to survive the subsequent 20–40 years of isolation. We then assume that a population of a size intermediate between the population size of the larger fragment (where the species still occurs) and the next smaller fragment (where the species is absent) marks the minimum size of a stable population that would survive for 20–40 years. For example: the theoretical population size of species A in a fragment of 400 ha is about 300 animals and the species is still found in a fragment of this extent. The theoretical population size of this species in a fragment of 200 ha is only 150 animals. Now if species A does not occur in the 200 ha fragment we assume that a population of 225 animals would not

be able to survive for about 20 years. This is the population size at which a species would be doomed to extinction if they were not able to exchange individuals with other areas. This minimum viable population and the average density of a given species was then used to calculate the minimum area of fragments for different lemur species that should allow them to survive for the next 20–40 years.

Table 2: Lemur species in differently sized forests (references as listed in table 1)

A: Littoral forest

Site	Area [ha]	<i>M</i> spp.	<i>C</i> spp.	<i>Hg</i>	<i>Al</i>	<i>Ef</i>	<i>L</i> spp.	<i>Dm</i>	<i>Pd</i>	<i>Er</i>	<i>Vv</i>	<i>li</i>
Body mass [kg]		0.04 - 0.06	0.13 - 0.4	0.8	1.1	2.25	0.6 - 0.9	2.5	6.6	2.0	3.75	6.75
Ambatovaki	>>	+	+	+	+	+	+	+	+	+	+	+
Anosyennes	>>	+	+	+	+	+	+	+	+			
Vohiminas	>>	+	+	+	+	+	+	+				
Tampolo	675	+	+	+	+	+	+					
Manafiafy S9	457	+	+	+	+	+						
Mandena M3	221	+	+	+	+	+						
Manafiafy S7	206	+	+	+	+	+						
Mandena M15/16	188	+	+	+	+	+						
Mandena M13	152	+	+	+	+	+						
Mandena M20	42	+	+		+							
Mandena M4	41	+	+	+								
Mandena M5	28	+	+									
Mandena M6	20	+	+									

B: Dry deciduous forest

Site	Area [ha]	<i>M</i> sp	<i>Pf</i>	<i>Mc</i>	<i>Lr</i>	<i>Cm</i>	<i>Ef</i>	<i>Pv</i>
Body mass [kg]		0.04- 0.06	0.4	0	0.8	0.13	2.25	3.6
Kirindi	>>	+	+	+	+	+	+	+
Menabe	600	+	+	+	+	+	+	+
Menabe	600	+	+	+	+	+		
Menabe	20	+	+					
Menabe	20	+	+		+			
Menabe	12	+	+	+				
Menabe	6	+	+	+	+			
Menabe	3	+						
Menabe	1	+						
Menabe	0.8							
Menabe	0.6							

Species: *Mspp.* = *Microcebus* spp., *Cm* = *Cheirogaleus medius*; *Cspp.* = *Cheirogaleus* spp.; *Mc* = *Mirza coquereli*, *Pf* = *Phaner furcifer*, *Lspp.* = *Lepilemur* spp., *Ef* = *Eulemur fulvus*, *Er* = *Eulemur rubriventer*, *Vv* = *Varecia variegata*, *Hg* = *Haplemur griseus*, *Al* = *Avahi laniger*, *Pv* = *Propithecus verreauxi*, *Pd* = *Propithecus diadema*, *li* = *Indri indri*, *Dm* = *Daubentonia madagascariensis*

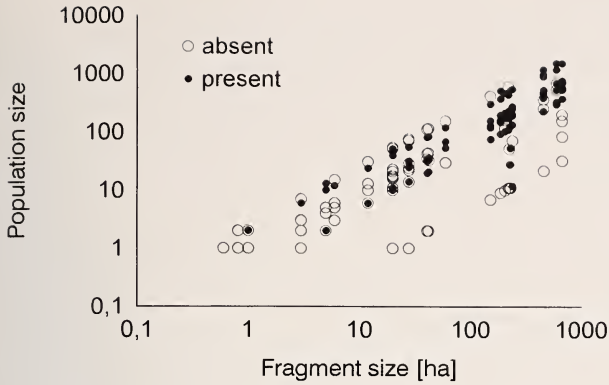


Fig.2: Theoretical population size of lemurs present in any one fragment at the time of isolation some 20–40 years ago. The different symbols mark whether or not the species in question is still present in a given fragment today.

Results and discussion

Presence/absence of lemurs in relation to forest type and size

The literature search revealed five studies that could be used to assess the effects of recent (20–40 year old) forest fragmentation on lemurs. The sources of these data and several parameters associated with each site are summarized in table 1.

Lemur species assemblages derived from littoral and dry forest lemur communities show highly nested patterns of species composition in fragments of declining size in both vegetation formations of Madagascar. This pattern held regardless of differences in the lemur communities in the large forested blocks that

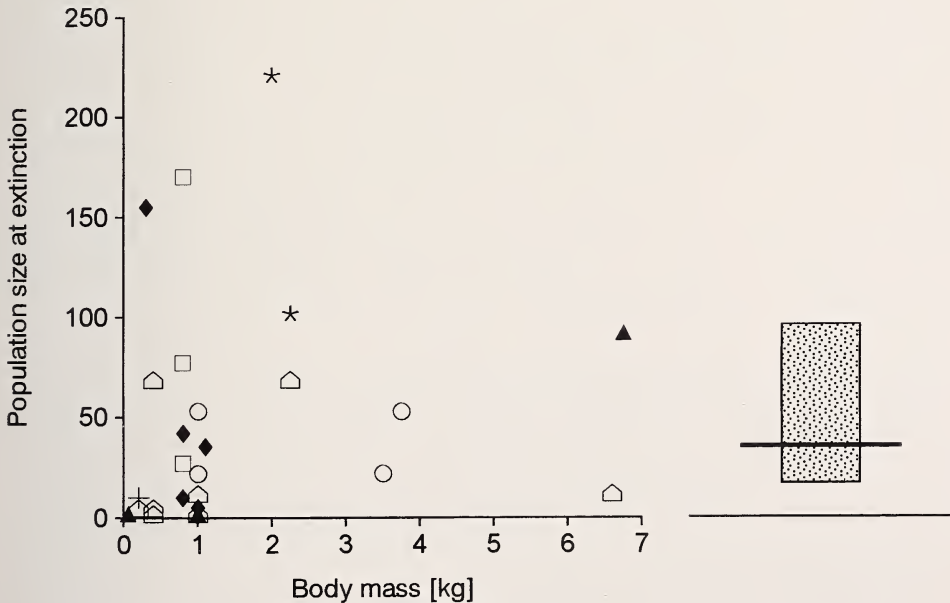


Fig. 3. Size of populations that were not viable for more than 20 – 40 years. On the right side the figure depicts the median and 25–75% quartiles of the non-viable mean population size for all species.

are considered to represent the original state (table 2). Both data sets deviate from random assemblages of species according to the analyses for nested data sets provided by Atmar & Patterson (1993: littoral forest: $T = 0.47$, $p < 0.001$; dry forest: $T = 0.17$, $p < 0.001$; based on 1000 runs). This pattern is repeated at all sites in Madagascar studied so far (Ganzhorn 1998).

Minimum viable populations

Fig.2 shows the presence/absence of lemurs in forest fragments of different size. Assuming that at the time the forest had been fragmented the lemur density in each fragment was equivalent to the average density of this species, we can estimate the number of individuals that were present in the fragment at the time of isolation. The probability of being present after 20–40 years of isolation correlates positively with increasing fragment size and decreasing body mass.

On average, populations of 36 adult individuals (median: 35.5; 25–75% quartiles: 17–97; $n = 13$ species) do not survive for more than 20–40 years (fig.3). The size of populations that are viable for 20–40 years is unrelated to body mass, litter size or inter-birth intervals. Minimum viable populations that can survive for 20–40 years seem to be smaller for folivorous and omnivorous species than for frugivorous species, though the effect is not significant due to small sample size.

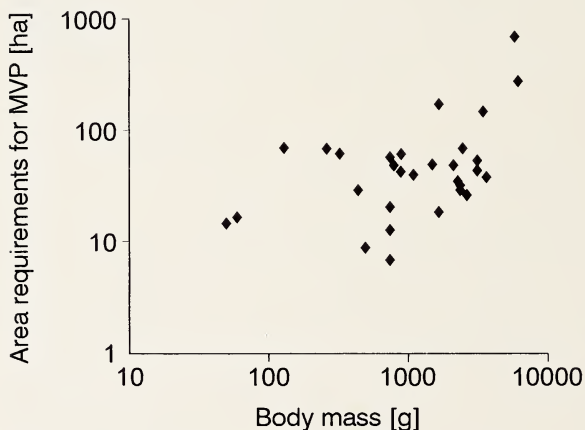


Fig.4: Minimum size of forest fragments to maintain viable populations of differently sized lemur species in the dry and in the humid forest.

The size of forest fragments required to maintain viable populations augments with increasing body mass and is larger for humid than for dry forests (fig.4). Thus, the small lemurs, such as *Microcebus* spp., need fragments of about 20 ha to survive for more than 20 years. But the largest lemurs of the eastern rain forest, such as *Indri indri* and *Propithecus diadema* which weigh up to about 7 kg (Mittermeier *et al.* 1994), need fragments of at least 8–10 km² to maintain viable populations for the period needed to establish new habitats for them - if indeed suitable habitats can actually be established. In the littoral forest sites of Mandena, Manafiafy and Tampolo there are no remaining fragments of that size. The largest known lemur species occurring in these forests is *Eulemur fulvus*, which weighs approximately 2.5 kg (Mittermeier *et al.* 1994). These littoral forests on sandy soils have low plant

productivity, which might contribute to their impoverished lemur communities as compared to adjacent forests on lateritic soils. This point is further complicated by the fact that the nearby sites with lateritic soils are still attached to the large eastern humid forest block.

The present analysis will have to be refined in the future as it rests upon a number of assumptions that do not take into account natural variation. But even if it were wrong by an order of magnitude, the future of the lemurs in Madagascar has to be a matter of grave concern.

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References

- Atmar, W. & B.D. Patterson (1993): The measure of order and disorder in the distribution of species in fragmented habitats. – *Oecologia* 96: 373-382.
- Britt, A., A. Axel & R. Young (1999): Brief surveys of two classified forests in Toamasina Province, eastern Madagascar. – *Lemur News* 4: 25-28.
- Du Puy, D.J. & J. Moat (1996): A refined classification of the primary vegetation of Madagascar based on the underlying geology: using GIS to map its distribution and to assess its conservation status. – pp. 205-218 in: *Biogeography of Madagascar* (ed. Lourenço, W. R.). – ORSTOM, Paris.
- Ganzhorn, J.U. (1987): A possible role of plantations for primate conservation in Madagascar. – *Amer. J. Primatol.* 12: 205-215.
- Ganzhorn, J.U. (1998): Nested patterns of species composition and their implications for lemur biogeography in Madagascar. – *Folia Primatol.* 69 (Suppl.): 332-341.
- Ganzhorn, J.U. & J.-P. Abraham (1991): Possible role of plantations for lemur conservation in Madagascar: food for folivorous species. – *Folia Primatol.* 56: 171-176.
- Ganzhorn, J.U. & J. Schmid (1998): Different population dynamics of *Microcebus murinus* in primary and secondary deciduous dry forests of Madagascar. – *Int. J. Primatol.* 19: 785-796.
- Ganzhorn, J.U., P.C. Wright & J. Ratsimbazafy (1999a): Primate communities: Madagascar. – pp. 75-89 in: *Primate communities* (eds. Fleagle, J.F., C. Janson & K. Reed). – Cambridge University Press, Cambridge.
- Ganzhorn, J.U., J. Fietz, E. Rakotovo, D. Schwab & D. Zinner

- (1999b): Lemurs and the regeneration of dry deciduous forest in Madagascar. – *Cons. Biol.* 13: 794-804..
- Goodman, S.M. & D. Rakotondravony (1998): Les lémuriens. – pp. 213-222 in: *Inventaire biologique de la Forêt littorale de Tampolo (Fenoarivo Atsinanana)*, Recherches pour le Développement, Série Sciences biologiques, Vol. 14, (eds. Ratsirarson J. & S.M. Goodman). – Centre d'Information et de Documentation Scientifique et Technique, Antananarivo.
- Goodman, S.M. & H. Schütz (1999): Observations of lemurs in the forest of Tsingoarivo, Ambatolampy. – *Lemur News* 4: 14-16.
- Green, G.M. & R.W. Sussman (1990): Deforestation history of the eastern rainforest of Madagascar from satellite images. – *Science* 248: 212-215.
- Holloway, L. (1999): Lemurs can't do it all by themselves anymore. – *Lemur News* 4: 29-30.
- Lamb, D. (1998): Large-scale restoration of degraded tropical forest lands: the potential role of timber plantations. – *Restoration Ecology* 3: 271-279.
- Lewis Environmental Consultants (1992): Madagascar Minerals Project. Environmental Impact Assessment Study. Part 1: Natural Environment. – Final Report to QIT Fer et Titane, Inc. Montreal, Quebec, Canada.
- Mittermeier, R.A., I. Tattersall, W.R. Konstant, D.M. Meyers & R.B. Mast (1994): Lemurs of Madagascar. – Conservation International, Washington, D.C.
- Nelson, R. & N. Horning (1993): AVHRR-LAC estimates of forest area in Madagascar, 1990. – *Int. J. Remote Sensing* 14: 1463-1475.
- Smith, A.P. (1997): Deforestation, fragmentation, and reserve design in western Madagascar. – pp. 415-441 in: *Tropical Forest Remnants, Ecology, Management and Conservation of fragmented Communities* (eds. Lawrence, W. & O.W. Bierregaard). – University of Chicago Press, Chicago.
- Sorg, J.-P. (1996): L'étude de la végétation, un outil au service de l'aménagement et de la gestion des ressources forestières à Madagascar. – *Akon'ny Ala* 18: 26-36.

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Priority areas for forest bird and primate conservation in Madagascar- do they match up?

Frank Hawkins

Abstract: Efforts to conserve biodiversity must be directed towards the most important areas. Aside from questions related to the feasibility of conservation, a key issue is the overlap of key areas (for species diversity or presence of threatened species) for different taxa. A premise of BirdLife International's **Important Bird Areas** project is that the distribution of threatened and restricted-range birds can be used as a surrogate for other, less well-known taxa.

In Madagascar, a recent study has identified 84 Important Bird Areas (IBAs), based on the presence of threatened, restricted-range and biome-restricted species. They are concentrated in primary forest and wetlands. The forest IBAs are concentrated in the north-eastern part of the humid forest, the north-western deciduous forest and parts of the southern spiny forest. A set of sites for primate conservation based on the presence of threatened species are concentrated in small patches of relict forest, mostly in the north and east, and in well-known sections of the eastern forest in the centre and south-east. There are no major priorities for primate conservation in the west or south. Using species richness as an indicator of conservation priorities gives a similar result. Thus overall there is no correlation between the priority rating of sites for bird and primate conservation, but with a few exceptions, the overall list of important bird areas includes all the important primate areas. This pattern is due, at least in part, to a lack of knowledge of taxonomy of nocturnal primate species, and poorly-known distributions of difficult-to-detect primates. In addition, the published threat categories of some widespread primate taxa seem inappropriate, partly because of the emphasis placed on taxonomic uniqueness.

However, even when these factors are allowed for, the distribution of primate and bird priority areas seems to differ because of fundamental differences in the patterns of regional endemism.

Key words: Important bird areas, Madagascar, primate conservation

The Madagascar context

Madagascar is widely regarded as one of the world's top biodiversity conservation priorities. Humans only arrived about 2000 years ago (MacPhee & Burney 1991), but are widely considered to have caused extensive deforestation (Green & Sussman 1990, Nelson & Horning 1993). It is certainly true that forests are being cleared today. This is resulting in the loss of an astounding array of endemic biological diversity. Around 12 000 species of plants, including 6 endemic families (Dupuy & Moat 1996), five families, 14 genera, 32 species and 50 taxa of primates, all endemic (Mittermeier et al. 1995); 106 species, 37 genera and 5 or 6 families of endemic bird (Morris & Hawkins 1998); about 300 reptile species, about 95% of which are endemic (Raxworthy & Nussbaum 1997). In addition, almost all this

diversity occurs in forest. About 80% of plant species are found only in forest, as are 33 of 37 endemic genera of bird. All extant primate taxa are exclusively forest dwelling (except one in a marsh).

Forest types

All forest types (which include eastern rainforest, western deciduous forest, and southern spiny forest) are declining in extent, probably fairly rapidly. The most threatened is probably western deciduous forest (Dupuy & Moat 1996). Eastern forest occurs along a north-south scarp, with most forest occurring where there are frequent dry-season nocturnal mists that prevent burning. Western and southern forests are rather patchy, and occur mostly in areas of low human population density.

Conservation issues

Madagascar is currently half way through the second phase of a fifteen-year three-phase National Environmental Action Plan (World Bank 1995). A workshop funded by the Global Environment Facility in 1995 produced an essential first step in defining conservation priorities for Madagascar (Ganzhorn et al. 1997). However, lack of accurate distribution detail for most taxa, and lack of ecological knowledge of how species' distributions vary with habitat, has prevented the development of a model that could be used for predicting conservation value of an area based on likely species presence (Hagen 1999). Such a model is essential if resources to make detailed inventories in all poorly-known forest areas are lacking. However, within the constraints of the National Environment Action Plan, there is a current urgent need to allocate scarce resources for the maximum biodiversity conservation good;

- Managers need a way of identifying sites that contain the maximum valuable biodiversity, for as many taxa as possible
- Managers would like to be able to use indicators to do this – species, families, higher taxa, habitats
- Managers need to know, for other taxa, where extra effort will be required outside these priority areas.

In Madagascar, only birds and primates are well enough known (at least in the published domain) for distributional comparisons to be useful. Thus in this paper the distributions of birds and primates are used to answer the following questions:

- What is the degree of overlap in sites containing the most threatened birds and primates?
- For birds and primates, if we choose a complement of sites that contains all key species for one taxon, which species in the other taxon are missed?
- Does the distribution of birds best represent the distribution of primates, or vice-versa?
- What are the implications of these results for conservation planning in the real world?

Methods

Two largely independent data sets were compared; birds and primates within the eastern rainforest biome, and birds and primates in the western and southern forest biome.

Priority sites for birds and primates were identified following the presence of threatened species (of IUCN categories: Critically Endangered, Endangered and Vulnerable, following Collar et al. 1994 and Mittermeier et al. 1994) present at a site. Bird distributions in potential priority areas came from 'Projet Zones d'Importance pour la Conservation des Oiseaux à Madagascar', a European Commission-funded collaboration between the Malagasy National Association for the Management of Protected Areas (ANGAP), the Ministry of Water and Forests (MEF), and BirdLife International (ZICOMA 1999). During Project ZICOMA, 117 sites were evaluated according to the presence of threatened, restricted-range or biome-restricted bird species. A book containing the details of the 84 sites (55 in forest) that qualified was published in July 1999.

Primate priorities were set using data from Ganzhorn et al. 1996, plus Projet ZICOMA recent sightings (ZICOMA 1999), S.M. Goodman's recent inventories for WWF (Goodman 1997, 1998, 1999, in press), and Conservation International's recent RAP studies (Schmid 1999, and this volume). This protocol was considered superior to one using simple species richness, as the non-threatened species not considered in this protocol are generally widespread, and present in most primary forests.

Complementarity analysis (Howard et al. 1998) used the "the simple greedy" algorithm (Williams 1998) which involves choosing a complementary set of sites within each major biome that included all the species of a particular taxon present in the biome.



Fig.1: Priority areas for bird and primate conservation in western Madagascar, defined by the presence of threatened species



Fig.2: Priority areas for bird and primate conservation in eastern Madagascar, defined by the presence of threatened species

Table 1: Top five western threatened primate priorities

Site	Number of taxa of threatened primate	Bird priority
RS Ankarana	7	8
RS Manongarivo	6	21
FC Andavakoera	5	13
Forêt Daraina	5	none
RS Analamera	5	3

Table 2: Top five western threatened bird priorities

Site	Number of species of threatened birds	Primate priority
RNI Ankarafantsika and SF Ampijoroa	2	9
PN Zombitse-Vohibasia	2	11
RS Analamera	2	4
Forêt Analavelona	2	23
Forêt Mikea- PK 32	2	none

Table 3: Top five eastern threatened primate priorities

Site	Threatened primates	Bird priority
PN Andringitra	9	11
PN Ranomafana	6	12
PN Mantady-RS Analamazaotra	6	3
RS Anjanaharibe-sud	5	7
PN Mananara-nord	5	26

Table 4: Top five eastern threatened bird priorities

Site	No of threatened species	Priority for primate conservation
PN Zahamena	12	10
PN Marojejy	11	7
PN Mantadia and RS Analamazaotra	10	5
PN Masoala	8	4
RNI Tsaratanana and surroundings	7	26

The first site chosen is that containing the most species within the biome. The second site is that containing the most remaining species, and so on. The congruence between these site complements was then evaluated by identifying the elements of the bird community present in the biome that were not present in the primate complement of sites, and vice-versa for the primates not present in the bird complement.

Results

Priority according to threatened species presence

Figs.1 and 2 show the distribution of priority sites in western and eastern Madagascar respectively. Western priority sites for primates are concentrated in the north, whereas those for birds show a much wider geographical spread. Bird priority sites in the east are concentrated in the north-east, whereas for primates there are two centres, in the north-east and in the south-east.

Tables 1-4 show that for birds and primates there is little correlation between priority sites, identified by the presence of threatened species.

Complementarity of taxa

Bird site complementarity

The eastern forest bird community is relatively homogenous, with most variation being accounted for by altitude (Hawkins, in press), and only three sites are necessary to include all the species - Zahamena, Amber Mountain and Ambatovaky (fig.1)

Bird communities in the west and south are more patchy; overlap is less well marked, but only two sites in each need to be chosen - Analavelona and Ankarafantsika (west) and Mikea and St Augustin (south) (fig.2).

Primate site complementarity

In the east, five sites are needed to include all the taxa (Anjanaharibe-sud, Masoala, Zahamena, Andringitra, Andohahela) (fig.1)

In the west, nine sites are needed to include all taxa (Ankarana, Analamera, Daraina, Manongarivo, Sahamalaza, Ankarafantsika, Katsepy, Bemaraha, Menabe) and in the south only one. The site used is Beza Mahafaly, as it includes large protected populations of the three locally endemic taxa, *Propithecus verreauxi verreauxi*, *Lemur catta* and *Lepilemur leucopus*. Many other sites containing these species could have been chosen (fig.2), including Mikea and St Augustin (the two bird sites representing southern populations), but at these sites the first two species occur in small and probably threatened populations.

Congruence

Forest bird taxa not present in the primate site complement

A total of eight species of birds, 28% of all threatened species, found in four different areas, are not to be found in the primate site complement:

Monias benschi, *Uratelornis chimaera* (Mikea)

Phyllastrephus apperti, *Monticola bensoni* (Analavelona)

Calicalicus rufocarpalis, *Coua verreauxi*, *Monticola imerinus* (Southwestern coastal forests)

Monticola erythronotus (Amber Mountain)

Primate taxa not present in the bird site complement

Sixteen primate taxa, 32% of all Malagasy primates, occurring in ten discrete forest areas, are not found in the complement of bird sites:

Microcebus "myoxinus", *Mirza coquereli* (Menabe)

Propithecus diadema perrieri (Analamera)

Propithecus diadema candidus (Anjanaharibe-sud, Marojejy)

Propithecus tattersallii (Daraina)

Propithecus verreauxi coronatus (Katsepy)

Propithecus verreauxi deckeni (Bemaraha)

Varecia variegata rubra (Masoala)

Haplemur aureus, *Haplemur simus*, *Eulemur fulvus albocollaris* (Andringitra)

Eulemur fulvus collaris (Andohahela)

Eulemur macaco macaco, *Lepilemur dorsalis*, *Phaner furcifer parienti* (Manongarivo)

Eulemur macaco flavifrons (Sahamalaza)

These results show that there is very little congruence between the distributions of restricted-range birds and primates in Madagascar. Patterns of endemism seem to be more similar within taxa rather than across them, as areas such as the Ranomafana - Andringitra corridor and the Sambirano (including Manongarivo) hold two species of locally endemic primate but no bird, and the Mikea Forest, the south-western forests, Analavelona-Zombitse-Isalo and (probably) Bemaraha all have at least two locally endemic bird species but no primate.

Discussion

Why are primate and bird priority sites so different?

Poor knowledge of distribution and taxonomy

It is possible that the disparity between bird and primate sites results at least in part from lack of knowledge of the distribution of certain taxa. In particular, it may be that populations of large *Haplemur* spp. exist in the north-east, and that *Allocebus trichotis* may be much more widespread. These taxa are difficult to detect, even for specialists. The taxonomy and distribution of *Microcebus* spp. are poorly known; at least two taxa have been described or rediscovered recently (Schmid & Kappeler 1994, Zimmermann et al. 1998). and there are probably several more (J. Schmid pers. comm. 1999). Amongst the birds, several taxa present in isolated massifs (for instance *Monticola* and *Canirallus* at Bemaraha, *Berniera* [= *Phyllastrephus*] "*zosterops*" *fulvescens* at Amber Mountain) appear to be good species. *Xenopirostris damii* was collected initially near the Bay of Ambaro, north-western Madagascar, and may be present elsewhere in this area. Resolution of these issues would not necessarily reduce the disparity in priority areas, however; Amber Mountain and Bemaraha are not centres of primate endemism, as far as is known.



Fig.3: Complement of sites for the conservation of birds in Madagascar

However, recent discoveries (e.g. *Calicalicus rufocarpalis*, Goodman et al. 1997), show that, as with primates (Ganzhorn et al. 1996) there are still surprising discoveries to be made even in apparently well-researched areas. Possibly discoveries of local bird and primate endemics have been made by specialists that would not recognise interesting forms outside their speciality, so that the presence of concentrations of endemic taxa of primate in certain areas might be a good basis for selecting priority areas for taxonomic research on birds, and vice versa.

Different responses to biogeographical changes (climate)

It appears that much of the recent biogeography of Madagascar has been dominated by climate change (Goodman & Rakotozafy 1997), which has produced forest "bridges" across the variably wooded central plateau during interglacial periods. Some of these bridges are shown in fig.3. Western and southern bird communities are probably largely derived from invasions of eastern founders across these bridges, and several local western and southern endemics (*Bernieria* [= *Phyllastrephus*] *apperti*, *Monticola bensoni*, *Monticola erythronotus*, *Monticola imerinus*, *Calicalicus rufocarpalis*, *Newtonia archboldi*) are probably recent splits from eastern montane species. Only *Uratelornis chimaera*, *Monias benschi*, and *Mesitornis variegata* seem to be ancient endemic inhabitants of the west, and even *M. variegata* has also recently been discovered in the east (Thompson & Evans 1992), confusing the question of its origin.

The pattern of recent western invasion is shown also in certain carnivores (*Galidia*, *Galidictis*, *Eupleres*) and at least one rodent (*Nesomys*), two subspecies of the generalist Brown lemur (*Eulemur fulvus rufus* and *E.f. fulvus*), and the



Fig.4: Complement of sites for the conservation of lemurs in Madagascar

generalist bamboo-eating primate *Haplemur griseus* (fig.4). However, other western, southern and northern primates seem less derivative; *Propithecus verreauxi* (with four subspecies), *P. tattersalli*, *Eulemur macaco*, *E. mongoz*, and *Mirza coquereli* all apparently lack close relatives in the east.

Two possible reasons for this pattern suggest themselves, and warrant further investigation; primates are probably less mobile in general than birds, and folivorous primates (e.g. *Propithecus*) may have small territories and be appear to be able to persist in small forest patches (for instance in Isalo National Park; Hawkins, in press a), which would promote their capacity to remain in relicts of forest left after climate change.

What are the implications for the priority-setting process?

There are already a series of conservation initiatives that cover a certain range of species. The taxa that are currently excluded from any formal protected area are:

Birds: *Monias benschi*, *Uratelornis chimaera*, (both Mikea Forest) *Calicalicus rufocarpalis* (southwestern forest);

Primates: *Propithecus tattersalli* (Daraina), *Eulemur macaco flavifrons* (Sahamalaza), *Propithecus verreauxi coronatus* (Katsepy, other forests between the Mahavavy and the Betsiboka).

In order for the ensemble of Malagasy primate and bird diversity to be conserved, these sites require conservation action urgently. In addition, three types of further study can be suggested. Firstly, surveys should be concentrated on complementary taxa in areas of endemism for birds and primates, to evaluate the true level of congruence. Secondly, in poorly-known areas or corridors between priority areas, rapid surveys of both birds and primates will give an initial indication of

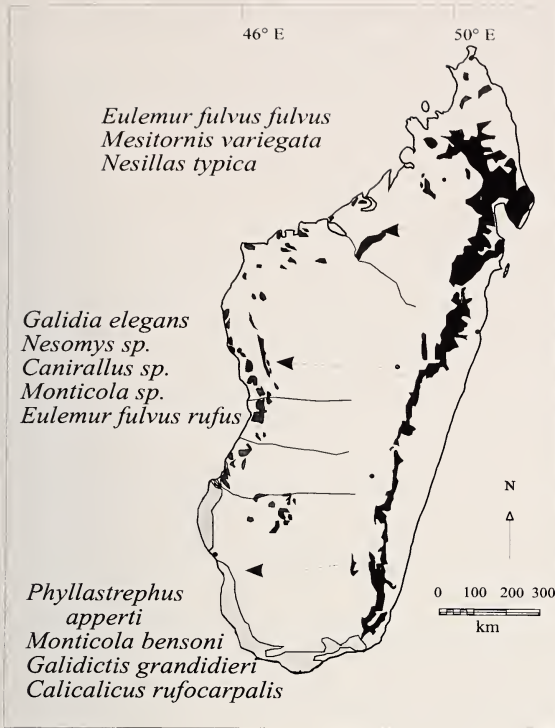


Fig.5: Madagascar, showing recent vegetation cover, positions of possible forest bridges and species likely to have moved along them.

comparative biodiversity value. Thirdly, once more detailed data sets are available for other taxa, particularly for reptiles and amphibians, complementarity analyses and studies of congruence with bird and primate data sets should be made.

Can we use habitat as an indicator of bird or primate conservation priority?

In the current "landscape conservation" paradigm, conservation or development projects are targeted at regions known to be important for conservation, but within which high priority areas are not yet identified. Clearly, in the case of western and northern Madagascar, where forests are so fragmented, any forest should be treated as a biodiversity priority and attempts made to evaluate in detail the biodiversity composition of these forests. In the east and south, however, forests are still fairly extensive, and any protocol that can help to identify priority habitats will be useful for regional planning. Given that bird communities in the east are relatively homogenous with latitude (Hawkins, in press b), and thus threatened bird species can generally be found wherever their preferred altitudinal forest type is present, it should be possible to set priorities for birds at an ecoregional scale in the east based on habitat. The most obvious case is the urgent need to include more lowland humid forest under some form of protection. However, distributions in the west and

south are more patchy, and the presence of a particular habitat cannot be used as an indication of the presence of a particular threatened species.

In the same way, primate priorities can be set in the east and south at a landscape level (for instance in between-river segments) based on habitat, but not in the west or north.

What are we left with?

Malagasy bird and primate conservation priorities show surprisingly little congruence, mostly as a result of differing patterns of local endemism.

Neither one can effectively act as a surrogate for the other in the identification of priority areas for conservation. However, using the combination of the two can give a preliminary list of priority sites for evaluation against other taxa. In addition, there are a number of very urgent site- and habitat-based priorities that come from the foregoing analysis, as well as an urgent need for more surveys in the areas and habitats indicated.

A comparison of priority areas for the combination of birds and primates with a set of priority areas for the conservation of reptiles and amphibians is the next obvious step – however, there are major problems in the identification of the latter, including lack of taxonomic stability, variation in detectability with season and weather, and difficulty of identification. These problems will probably only be resolvable following much more intensive study and analysis of the distribution of Malagasy reptiles and amphibians.

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References

- Green, G.M. & R.W. Sussman (1990): Deforestation history of the eastern rain forests of Madagascar from satellite images. – *Science* 248: 213-215.
- Collar, N.J., M.J. Crosby & A. Stattersfield (1994): *Birds to Watch*. Second edition. – BirdLife International, Cambridge, U.K..
- Dupuy, D.J. & J. Moat (1996): A refined classification of the primary vegetation of Madagascar based on the underlying geography: using GIS to map its distribution and to assess its conservation status. – pp. 205-218 in: *Biogéographie de Madagascar*. (ed. Laurenço, W.R.) – Paris: Editions de l'ORSTOM.
- Ganzhorn, J.U., O. Langrand, P.C. Wright, S. O'Connor, B. Rakotosamimanana, A.T.C. Feistner & Y. Rumpler (1996): The state of lemur conservation in Madagascar. – *Primate Conservation* 17: 70-80

- Ganzhorn, J.U., B. Rakotosamimana, L. Hannah, J. Hough, L. Iyer, S. Olivieri, S. Rajaobelina, C. Rodstrom & G. Tilkin (1997): Priorities for biodiversity conservation in Madagascar. – *Primate Report* 48: 1-25.
- Goodman, S.M. (ed) (1997): A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar; with reference to elevational variation. – *Fieldiana, Zoology*, new series 85.
- Goodman, S.M. (ed.) (1998): A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar; with reference to altitudinal variation. – *Fieldiana Zoology*, new series 90: 1-241.
- Goodman, S.M. (ed.) (1999): A floral and faunal inventory of the Parc Nationale d' Andohahela, Madagascar; with reference to elevational variation. – *Fieldiana Zoology*, new series.
- Goodman, S.M. (ed.) (in press): A floral and faunal inventory of the Parc Nationale de Marojejy, Madagascar; with reference to elevational variation. – *Fieldiana Zoology*, new series.
- Goodman, S.M., A.F.A. Hawkins & C.A. Domergue (1997): A new species of *Vanga* (Vangidae) from south-western Madagascar. – *Bull. Brit. Ornithol. Cl.* 117: 5-10.
- Goodman, S.M. & L.M.A. Rakotozafy (1997): Subfossil birds from coastal sites in western and southwestern Madagascar: a palaeoenvironmental reconstruction. – pp. 257-279 in: *Natural Change and Human Impact in Madagascar* (eds. Goodman, S.M. & B.D. Patterson). – Smithsonian Institution, Washington.
- Hagen, R. (1999): Biodiversity conservation priorities in the three regions of the Landscape Development Interventions Program. – Unpublished report to USAID Madagascar.
- Howard, P.C., P. Viskanec, T.R.B. Davenport, F.W. Kigenyi, M. Baltzer, C.J. Dickinson, J.S. Lwanga, R.A. Matthews & A. Balmford (1998): Complementarity and the use of indicator groups for reserve selection in Uganda. – *Nature* 394:472-475.
- Hawkins, A.F.A. (in press a): The primates of Isalo National Park, Madagascar. – *Lemur News*.
- Hawkins, A.F.A. (in press b): Altitudinal and latitudinal distribution of east Malagasy forest bird communities. – *J. Biogeogr.*
- MacPhee, R.D.E. & D.A. Burney (1991): Dating of modified femora of extinct dwarf *Hippopotamus* from southern Madagascar: implications for constraining human colonisation and vertebrate extinction events. – *J. Archaeol. Sci.* 18: 695-706.
- Morris, P.A.J & A.F.A. Hawkins (1998): A photographic fieldguide to the birds of Madagascar. – Pica Press, Robertsbridge, East Sussex.
- Nelson, R. & N. Horning (1993): AVHRR-LAC estimates of forest area in Madagascar, 1990. – *Int. J. Remote Sensing* 14:1463-1475
- Mittermeier, R.A., I. Tattersall, W.R. Konstant, D.M. Meyers & R.B. Mast (1994): *Lemurs of Madagascar*. – Conservation International,

Washington, D.C..

- Raxworthy, C.J. & R.A. Nussbaum (1997): Biogeographic patterns of reptiles in eastern Madagascar. – pp. 124-141 in: Natural Change and Human Impact in Madagascar (eds. Goodman, S.M. & B.D. Patterson). – Smithsonian Institution, Washington.
- Schmid, J. & P.M. Kappeler (1994): Sympatric mouse lemurs (*Microcebus* spp.) in Western Madagascar. – *Folia Primatol.* 63: 162-170.
- Schmid, J. (ed) (1999): Rapport préliminaire d'inventaire rapide, corridor Mantadia- Zahamena. – Conservation International, Madagascar.
- Thompson, P.M. & M.I. Evans (1992): The threatened birds of Ambatovaky Special Reserve, Madagascar. – *Bird Conserv. Int.* 2: 221-237.
- Williams, P.H. (1998): Key sites for conservation: area-selection methods for biodiversity. – pp. 211–249 in: Conservation in a Changing World: Integrating Processes into Priorities for Action (eds. Mace, G.M., A. Balmford & J.R. Ginsberg). – Cambridge University Press, Cambridge, UK.
- World Bank (1995): Madagascar Environment Program Staff Appraisal Report. – World Bank, New York, USA.
- ZICOMA (1999): Zones d'Importance pour la Conservation des Oiseaux à Madagascar. – Projet ZICOMA, Antananarivo, Madagascar, 266pp.
- Zimmermann, E., S. Cepok, N. Rakotoarison, V. Zietemann & U. Radespiel (1998): Sympatric mouse lemurs in north-west Madagascar: a new rufous mouse lemur species (*Microcebus revelobensis*). – *Folia primatolog.* 69: 106-114.

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Conservation planning in the Mantady-Zahamena corridor, Madagascar: Rapid Assessment Program (RAP)

Jutta Schmid

Abstract: Conservation International (CI) conducted a Rapid Assessment Program (RAP) of the biodiversity of the humid forest within the Mantady-Zahamena corridor in Madagascar. The RAP methodology is designed to quickly provide information needed to catalyze conservation activity and improve regional and national biodiversity protection. This eastern mountain range corridor links the protected areas of the Parc National (PN) de Mantady and the Réserve Naturelle Intégrale (RNI) de Zahamena. This region is of particular interest and importance since not only does it comprise of primary and secondary lowland rainforest as well as moist montane forest, but it also connects two protected areas in the north and south. Survey work was divided into two expeditions (expedition 1: November 7 – December 14, 1998; expedition 2: January 15 – 28, 1999). Four camps were placed in different classified forests, and one site was placed in PN de Mantady. At each site, presence and relative abundance of lemur species were estimated using the line transect method. A total of 11 lemur species (four diurnal, two crepuscular, and five nocturnal species) were found in the corridor, including Aye-Aye *Daubentonia madagascariensis*. Forest clearance and settlement in the entire corridor are the major threats and might explain relatively low densities and absence of certain lemur species like *Propithecus diadema diadema* (site 1) and *Varecia variegata variegata* (site 1 and 5). Exceptional biodiversity cannot be maintained in areas where genetic exchange is impossible due to geographic isolation and disconnection of forest blocks. The most urgent and basic need is to stop forest fragmentation and habitat destruction, and to place exceptionally high conservation priorities on remaining lowland forests.

Key words: Madagascar, Rapid Assessment Program, lemurs, conservation

Introduction

Endemism in Madagascar's biota is extremely high, with species-level endemism of well over 90% for most taxonomic groups (Jenkins 1987, Langrand & Wilme 1997). One of the major adaptive radiations in Madagascar is among the primates. Malagasy lemurs (comprising about 33 species and 52 subspecies) are entirely endemic and occupy a wide range of forests, including eastern humid forests, western dry forests, and southern spiny forests (Harcourt & Thornback 1990, Mittermeier et al. 1994, Tattersall 1982). However, it is estimated that as much as 80% of these forests has disappeared in the 1500-2000 years since the arrival of man, to open land up for agricultural purposes, for mining, for extraction of building materials and fuelwood, and for commercial logging (Nelson & Horning 1993; Smith et al. 1997).

Forest fragmentation and habitat loss affect species richness and diversity (Laurance 1991), as they can cause changes in species-specific population dynamics. Reestablishment of the original biodiversity of isolated forest patches depends on distances to other wooded areas, and presence of fencerow connections (Gascon & Lovejoy 1998, Lindenmayer et al. 1993). Isolation of forested habitat may restrict rates of migration, and initially produce increases in density relative to continuous forest sites (Gascon & Lovejoy 1998). So far, little is known about possible consequences of disrupted gene flow and inbreeding in small populations for the long-term survival of these species (Tomiuk et al. 1998). Corridors between remaining blocks of forest are required to maintain gene flow, facilitate the movement of animals across inhospitable terrain and promote dispersal between disjunct patches of habitats (Lindenmayer et al. 1993, Saunders et al. 1991, Tomiuk et al. 1998). Given the ongoing fragmentation of the Malagasy forests, corridors will be important for the survival of lemur species in otherwise fragmented habitats.

Successful conservation planning for the unique habitats of Madagascar must be based on information on the biological resources existing in the region. Baseline inventory data can be obtained through "rapid assessments". Conservation International's Rapid Assessment Program (RAP) is designed to quickly provide the scientific information needed to catalyze conservation activity and improve regional and national biodiversity protection. RAP assembles teams of scientists to generate first-cut assessments of the biological value of poorly known areas.

The Madagascar RAP expedition was conducted in the non-protected corridor between the Réserve Naturelle Intégrale (RNI) de Zahamena (to the north) and the Parc National (PN) de Mantady (to the south) in the eastern humid forest of Madagascar (Nicoll & Langrand 1989). As part of this multi-taxa inventory expedition, data were collected on primate species richness and abundance at four different sites within the corridor, as well as at one site in the PN de Mantady. Information on the distribution and density of lemur species in the Mantady-Zahamena region and the degree of threat to these populations is important to manage this part of Madagascar's rainforests in the context of an integrated conservation and development project.

Methods

Preparatory work and planning

In August and September 1998, local Malagasy stakeholders were interviewed to determine the specific types of data they desire, and to identify areas within the corridor of highest priority for biodiversity conservation. After that, recent vegetational and topographical maps (Ministère de l'Agriculture et du Développement Rural 1997, FTM 1968) of the area targeted for the RAP assessment were consulted to determine the extent of forest cover and likely areas for exploration. On October 12th 1998, an overflight in a small plane was conducted to identify forest types and points for field transects. Finally, ground reconnaissances were carried out to determine study sites, the route to be used for the transects and to prepare transport and logistics.

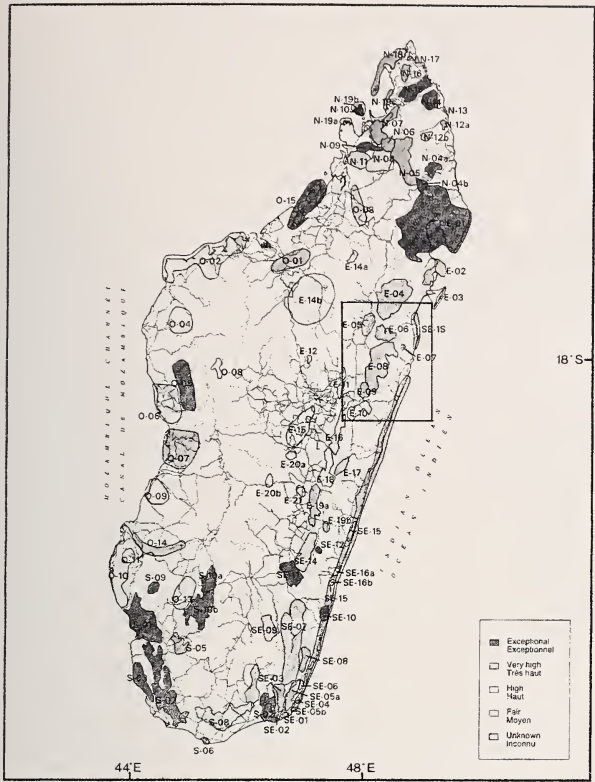


Fig.1: Map of Madagascar with areas of high biological importance. The area of the RAP is indicated. (From Ganzhorn et al. 1997)

Study sites

The biological inventory was conducted at five sites in the humid forest of the Mantady-Zahamena corridor (fig.2). The study sites were determined with the use of an overflight video, geographical and vegetational maps, and consultations with local people and national stakeholders. Survey work was divided into two expeditions (expedition 1: site 1 to 4: November 7 to December 14, 1998; expedition 2: site 5: January 15 to 28, 1999). Transects were centered around these sites within a radius of approximately 1.5 kilometers. Sampling lasted 6–7 days at each site. Names and positions of the five sites surveyed during the RAP are presented in table 1.

Table 1: Names and positions of sites surveyed during the RAP

Name of the site	Location	Altitude	Status*	Time period
Iofa (Site 1)	18°42.1'S, 48°28.0'E	835 m	FC	07-13 Nov
Didy (Site 2)	18°11.9'S, 48°34.7'E	960 m	FC	16-22 Nov
Mantady (Site 3)	18°47.5'S, 48°25.6'E	895 m	PN	25 Nov-01 Dec
Andriantantely (Site 4)	18°41.7'S, 48°48.8'E	530 m	FC	04-10 Dec
Sandranantitra (Site 5)	18°02.9'S, 49°05.5'E	450 m	FC	18-24 Jan

*) FC = Classified forest; PN = National Park

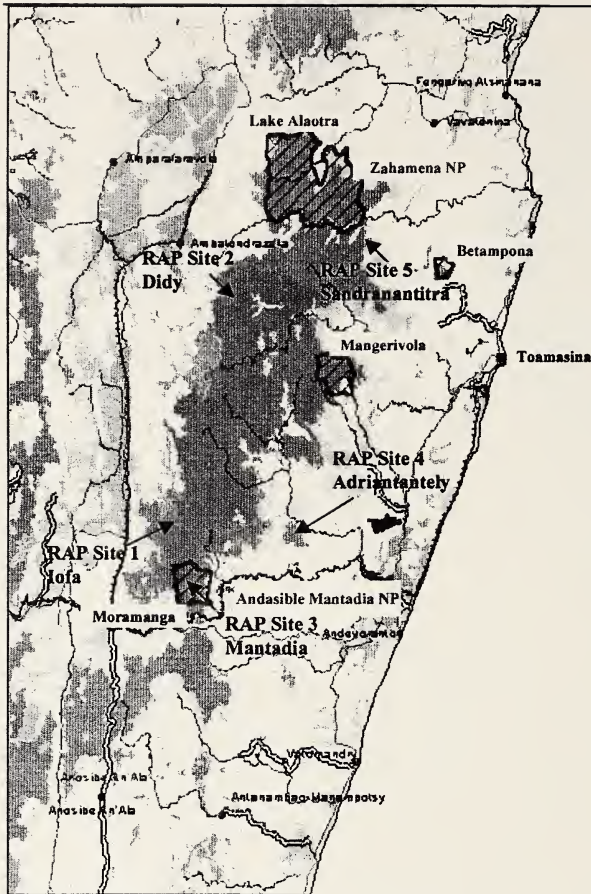


Fig.2: Location of the study sites. Hatched areas indicate protected areas.

Line transects

The line transect method was employed for censusing lemurs. At each location two or three trails of varying lengths (750 m to 2700 m) were used for lemur surveys. We utilized preexisting trails left by bush pigs, cows and humans, as well as newly cut and laid out trails. Lemurs were censused by walking slowly (approximately 0.7 km h^{-1}) along trails marked at 25 m cumulative intervals with flagging tape. Diurnal samples took place at times of increased lemur activity, in the morning (6:00 – 12:30h) and in the afternoon (15:00 – 18:00 h). Walks were always separated by a time interval of at least six hours when trails were censused twice during daylight hours. Nocturnal censuses commenced 10 to 30 minutes after dusk for two to four hours each night. The dim light of a headlamp was used at night to pick up the eyeshine from the reflective tapetum of nocturnal lemurs. Once detected, a more powerful hand-held flashlight and binoculars (7x40) were used for species identification.

For all detections, the species, time of contact, position on the transect, elevation, perpendicular distance from the trail, height from the ground, and habitat type were noted. Whenever possible, the number of individuals, age/sex composition and general behavior were also recorded. For each group of lemurs we estimated the perpendicular distance from the trail for the first individual seen. We did not spend more than 10 minutes on any single sighting. Censusing along each transect was repeated 1–3 times for nocturnal transects and 2–9 times for diurnal transects. Census walks were not conducted when viewing distance was restricted to less than 15 m because of heavy rain.

Due to inadequate sample sizes because of the few repetitions of each transect, and the relatively short distances covered at each site, lemur densities were not determined (Ganzhorn 1994; Schmid & Smolker 1998; Sterling & Ramarason 1996; Whitesides et al. 1988). However, we did calculate the mean number of sightings of lemurs per km transect and the mean detection distance perpendicular to the trail at which lemurs were seen was given for each species and trail. Since we did not find significant differences across trails, a single average detection distance was calculated for each species. For diurnal censuses the mean number of groups, and for nocturnal censuses the mean number of individuals observed within the transects were given. Lemurs heard but not seen during census walks, or seen outside of census walks by ourselves or other researchers, were not included in our calculations of encounter rates for either diurnal or nocturnal surveys.

General observations

Apart from the systematic transect surveys general observations were made during the day. At each site we explored the forest to look for secondary signs of the presence of certain lemurs such as the characteristic feeding signs of *Daubentonia madagascariensis* (gnaw marks from excavation of dead wood or living branches, opened seeds of *Canarium madagascariense*), or sleeping sites of nocturnal species (e.g. nests of *Daubentonia*; tree holes of *Cheirogaleus* or *Microcebus*). Furthermore, we paid special attention to vocalizations (songs) of Indris (*Indri indri*) and Ruffed Lemurs (*Varecia variegata*). Local people were questioned to collect information about the presence of lemur species and about the hunting pressure on the primate fauna.

Results

Species diversity

In total, four diurnal species (*Indri indri*, *Propithecus diadema diadema*, *Varecia variegata variegata*, and *Eulemur rubriventer*), two crepuscular species (*Eulemur fulvus fulvus* and *Hapalemur griseus griseus*), and five typically nocturnal species (*Microcebus rufus*, *Cheirogaleus major*, *Avahi laniger*, *Lepilemur mustelinus*, and *Daubentonia madagascariensis*) were found in five survey sites within the Mantady-Zahamena corridor (table 2). All taxa were recorded by direct observation except for *Daubentonia*, which was recorded by its indirect feeding signs (Duckworth 1993, Erickson 1995). None of the five survey sites contained all species. Species diversity was highest at sites 2 and 3, where ten lemur species were present. Eight species were found at sites 1 and 4, and only six at site 5. *Indri indri*,

Table 2: The primate species found in the humid forests of the Mantady-Zahamena corridor listed by camp site and altitude. Species were recorded during survey walks or during additional observations.

	Site 1 835 m	Site 2 960 m	Site 3 895 m	Site 4 530 m	Site 5 450 m
<i>Microcebus rufus</i>	+	+	+	+	+
<i>Cheirogaleus major</i>	+	+	+	+	+
<i>Avahi laniger</i>	+	+	+	+	
<i>Lepilemur mustelinus</i>	+	+	+		+
<i>Daubentonia madagascariensis</i>					fd
<i>Indri indri</i>	#	+	+	+	*
<i>Propithecus diadema diadema</i>		+	+	+	
<i>Varecia variegata variegata</i>	0	#	#	+	
<i>Eulemur rubriventer</i>		+	+		
<i>Eulemur fulvus fulvus</i>	#	+	+	+	+
<i>Haplemur griseus griseus</i>	0	+	+	+	
Total number of species	8	10	10	8	6

+ species present; # species seen by other participants; fd feeding signs; * vocalizations only

Table 3: Mean number of sightings per km transect and mean detection distances (\pm standard deviation) of species (individuals) seen during nocturnal censuses at each camp site in the Mantady-Zahamena corridor. Detection distances are perpendicular to the trail; n = number of individuals.

Trail	Length of transects (m)	Number of censuses	<i>Microcebus rufus</i>	<i>Cheirogaleus major</i>	<i>Avahi laniger</i>	<i>Lepilemur mustelinus</i>	Number of species
1-T1	1300	2	0.6 (1.0)	0.6 (3.0)		0.6 (2.0)	3
1-T2	1000	2	0.5 (3.0)	4.5 (6.0 \pm 3.1)	1.0 (3.0)	1 (8.0)	4
1-T3	750	2					0
2-T4n	1400	3	2.4 (3.4 \pm 1.6)	1.0 (4.4 \pm 2.8)	0.5 (3.8 \pm 0.4)	0.2 (8.0)	4
2-T5	1400	2	1.4 (3.1 \pm 2.1)	1.1 (5.3 \pm 2.5)		0.7 (3.3 \pm 1.1)	3
3-T6n	1800	3	0.6 (0.8 \pm 0.6)	0.4 (3.0 \pm 1.4)	0.4 (3.3 \pm 1.1)	0.7 (2.3 \pm 1.4)	4
3-Tm	2500	2	1.4 (3.9 \pm 1.8)	1.2 (5.1 \pm 4.2)	0.4 (1.5 \pm 0.7)	0.8 (2.3 \pm 0.5)	4
4-T8	1700	2		0.3 (1.0)	0.3 (2.0)		2
4-T9	1800	1	0.6 (2.0)	0.6 (4.0)	0.6 (3.0)		3
5-T10	1800	3	1.3 (2.8 \pm 2.3)	1.3 (5.7 \pm 3.4)		0.2 (0.2)	3
5-T11	1500	1	1.3 (2.5 \pm 0.5)				1
Mean detection distance (m)			3.0 \pm 1.8 n = 36	5.1 \pm 3.1 n = 34	3.0 \pm 1.3 n = 9	3.1 \pm 2.3 n = 14	

E. f. fulvus, *M. rufus* and *C. major* were found at all sites surveyed. *H. griseus*, *V. v. variegata* and *A. laniger* were absent from site 5, and *L. mustelinus* was censused at all sites except site 4. *P. d. diadema* was seen from site 2 to 4. *E. rubriventer* occurred only in the mid-altitude forests of site 2 and 3, but no evidence for its presence was found at site 1 (835 m). *D. madagascariensis* was only present in the forest of Sandranantitra (site 5). Of particular interest was the extremely high encounter rate of *V. v. variegata* at site 4, where at least six different groups along a total trail length of 2.5 km were found. The length of transects, number of census walks and the species encountered at the various sites are listed in table 3 for nocturnal censuses and in table 4 for diurnal censuses. During night surveys a total of 35.6 km was walked, and 98.7 km during the day surveys.

Table 4: Mean number of sightings per km transect and mean detection distances (\pm standard deviation) of species (individuals and groups respectively) seen during diurnal censuses at each camp site in the Mantady-Zahamena corridor. Detection distances are perpendicular to the trail; n = number of groups.

Trail	Length of transects (m)	Number of censuses	<i>Indri indri</i>	<i>Propithecus diadema diadema</i>	<i>Varecia variegata variegata</i>	<i>Eulemur rubriventer</i>	<i>Eulemur fulvus fulvus</i>	<i>Hapalemur griseus griseus</i>	Number of species
1-T1	1300	5	0		0		0	0.3 (4.5 \pm 3.5)	4
1-T2	1000	6	0					0.3 (4.5 \pm 3.4)	2
1-T3	750	5	0						1
2-T4	2600	7	0	0.1 (6.0)	0	0.1 (1.5 \pm 0.7)	0.1 (4.0)	0.2 (5.3 \pm 3.3)	6
2-T5	1400	4	0		0		0.2 (10.0)		3
3-T6	2700	9	0.1 (5.3 \pm 4.5)	0.1 (2.0 \pm 1.4)	0	0.04 (12.0)		0.1 (5.0 \pm 1.7)	5
3-Tm	2500	2	0	0.2 (12.0)	0		0.2 (8.0)		4
4-T8	1700	5	0.4 (9.7 \pm 9.1)		1.6 (6.0 \pm 3.1)		0	0	4
4-T9	1800	4	0.1 (1.0)	0.1 (5.0)	0.8 (6.2 \pm 4.4)			0.3 (8.0 \pm 9.9)	4
5-T10	1800	6	0				0.2		2
5-T11	1500	3	0				0		2
Overall mean detection distance (m)			6.6 \pm 6.7 n = 7	5.4 \pm 4.2 n = 5	6.1 \pm 3.4 n = 20	5.0 \pm 6.1 n = 3	7.0 \pm 2.4 n = 5	5.4 \pm 3.9 n = 13	

* species heard or seen outside predefined census walks.

Discussion

The Mantady-Zahamena corridor represents an important area for lemurs, and both species diversity and relative abundance is remarkable. Eleven species were confirmed in the corridor and in the PN de Mantady: ten species were detected by direct sightings on census walks and the presence of Aye-aye *Daubentonia madagascariensis* can be inferred from distinctive feeding traces.

The forest block surveyed borders to the north on the RNI de Zahamena, and to the south on the PN de Mantady. This corridor contains a complex network of classified forests, commercial forestry zones, local forest exploitation and two other reserves, Mangerivola and Betampona. The entire region within and between

these protected areas is extremely important for biodiversity conservation purposes. According to IUCN criteria, six of the 11 species recorded in the corridor are considered to be globally threatened by extinction (Harcourt & Thornback 1990). Although no quantitative assessment of lemur population densities was made, total number as well as relative abundance of species differed between sites. The number of species decreased from ten species recorded at sites 2 and 3, to eight at sites 1 and 4, and finally reached a minimum of only six species at site 5. Forest clearance and settlement in the entire corridor are the major threats and might explain relatively the low densities and absence of particular lemur species like *P. d. diadema* (site 1) or *V. v. variegata* (sites 1 and 5). Of particular interest was the low diversity and abundance of lemur species in the lowland forests of Sandranantitra compared to all the other sites surveyed. Numerous clearings and trails have already penetrated into this forest, and lemur traps, although always inactive, were frequently found, indicating that hunting pressure is another major threat to this area and its lemur populations. By contrast, in areas within the Mantady-Zahamena corridor, where deforestation and consequently hunting pressure on lemurs was relatively low (sites 2, 3 and 4), the present diurnal lemur species were remarkably tolerant of humans, tending to approach at close range or to simply ignore them.

The result of the overflight indicated that the lowland forest of Andriantantely is an isolated remnant in contrast to the remaining survey sites which were all still connected to adjacent rainforest. With eight lemur species found in Andriantantely, this forest had a higher diversity of primates than the lowland forest of Sandranantitra where only six species were found. Although Sandranantitra was characterized by a high degree of habitat destruction, it has not been isolated from the mid-altitude mountain forest chain to its west. However, the results of the plant and vegetation survey, which was undertaken simultaneously, indicated that Sandranantitra forest must have suffered a dramatic deforestation and probably defaunation a long time ago. The forest of Sandranantitra was dominated by large trees of *Ravenala madagascariensis* (Strelitziaceae) indicating that this forest was previously exploited. By contrast, Andriantantely contains ca. 7,000 ha of primary lowland forest that has been isolated for only several years, and it still maintains viable populations of its original lemur richness and abundance. Clearly, forest fragmentation does have an impact on the original community, with many species that may persist for long periods after isolation, but other species that may eventually get lost (Kattan et al. 1994, Laurance 1991, Turner 1996). Andriantantely may be in a very early stage of isolation and thus possible consequences are not yet discernible, whereas in Sandranantitra certain lemur species have already retreated to undisturbed adjacent forests.

Mittermeier et al. (1992) list already protected lowland forests as areas which are of highest priority for the immediate establishment of programs for conservation action. However, conservation of protected areas with a notably diverse and dense lemur population, such as Zahamena with 14 lemur species or Mantady with ten lemur species, only makes sense when trans-frontier areas and corridors are included in conservation planning. Exceptional biodiversity cannot be maintained in areas where genetic exchange is impossible due to geographic isolation and disconnection of forest blocks (Ganzhorn et al. 1996/1997, Lindenmayer et al.

1993, Rabarivola et al. 1996, Saunders et al. 1991). Since we do not have more detailed information on natural gene flow and genetic differentiation in isolated populations of certain lemur species, fragmentation processes need to be reduced.

Experience to date in Madagascar demonstrates that success in preserving and managing protected areas and classified forests is highly dependent on improving the management of critical habitats for biodiversity and on addressing the economic pressures on these ecosystems from neighboring communities (Mittermeier et al. 1987, 1994, Richard & O'Connor 1997). Adjacent regions around the Mantady-Zahamena corridor are of great economic importance, with Moramanga in the south, Toamasina on the eastern coast, and the Lac Alaotra region to the west, which include the biggest lake and principal rice-producing area in Madagascar. Madagascar is one of the poorest countries in the world, and rapid population growth is one of the main causes of natural resource degradation. Thus conservation of Madagascar's biodiversity can only be successful if it includes economic improvements for local communities.

From the point of view of diversity and density of lemur species, the Mantady-Zahamena corridor has to be considered a priority area. The most urgent and basic need is to stop forest fragmentation and habitat destruction, and to place exceptionally high conservation priorities on remaining lowland forests. For this, we suggest the following recommendations aimed at activities for lemur conservation:

- Lemur conservation can only be successful if we find ways of allowing the coexistence of humans and lemurs. Tree plantations could provide firewood, fruit, honey and building material for people as well as suitable habitat for lemurs, and would guarantee that the pressure on the natural forests is reduced.
- Malagasy primatologists have to be promoted and trained in representing and spreading the word on the importance of lemurs and their natural habitat to the Malagasy public and government institutions. This is of particular importance since there is a strong awareness against conservation projects among governmental and non-governmental organizations. Workshops and seminars undertaken by Malagasy and international experts could train individuals in data collection and analysis, database management, and the geographic information system (GIS).
- Community education programs and socio-economic research should be undertaken.
- Information on the genetic population structure, population dynamics, possible consequences of disrupted gene flow and inbreeding in small populations is desperately needed for the long-term survival of lemurs. These data are needed to interpret the biological importance of genetic differentiation and variation and their possible value to the survival of lemurs in isolated forest fragments.

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References

- Bennett, A.F., K. Henein & G. Merriam (1994): Corridor use and the elements of corridor quality: chipmunks and fencerows in a farmland mosaic. – *Biol. Conserv.* 68: 155-165.
- Duckworth 1993 [s.S. 6]
- Duckworth, J.W., M.I. Evans, A.F.A. Hawkins, R.J. Safford & R.J. Wilkinson (1995): The lemurs of Marojejy Strict Nature Reserve, Madagascar: A status overview with notes on ecology and threats. – *Int. J. Primatol.* 16: 545-559.
- Erickson, C.J. (1995): Feeding sites for extractive foraging by the aye-aye, *Daubentonia madagascariensis*. – *Am. J. Primatol.* 35: 235-240.
- Ganzhorn, J.U. (1994): Les lémuriens. – pp. 70-72 in: Recherches pour le Developpement: Inventaire Biologique de la Forêt de Zomibtse, vol. spécial (eds. Goodman, S.M. & O. Langrand). – Centre d'Information et de Documentation Scientifique et Technique, Antananarivo.
- Ganzhorn, J.U., O. Langrand, P.C. Wright, S. O'Connor, B. Rakotosamimanana, A.T.C. Feistner & Y. Rumpler (1996/1997): The state of lemur conservation in Madagascar. – *Primate Conserv.* 17: 70-86.
- Gascon & Lovejoy 1998 [s.S. 2]
- Harcourt, C. & J. Thornback (1990): Lemurs of Madagascar and the Comoros. – Gland, Switzerland and Cambridge, U.K.
- Henderson, M.T., G. Merriam & J. Wegner (1985): Patchy environments and species survival: Chipmunks in an agricultural mosaic. – *Biol. Conserv.* 31: 95-105.
- Jenkins 1987 [s.S. 1]
- Kattan G.H., H. Alvarez-López & M. Giraldo (1994): Forest fragmentation and bird extinctions: San Antonio eighty years later. – *Conserv. Biol.* 55: 269-281.
- Langrand & Wilme 1997 [s.S. 1]
- Laurance, W.F. (1991): Ecological correlates of extinction proneness in Australian tropical rain forest mammals. – *Conserv. Biol.* 5: 78-89.
- Lindenmayer, D.B., R.B. Cunningham & C.F. Donnelly (1993): The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-east Australia, IV. The presence and abundance of arboreal marsupials in retained linear habitats (wildlife corridors) within logged

- forest. – *Biol. Conserv.* 66: 207-221.
- Mittermeier, R.A., W.R. Konstant, M.E. Nicoll & O. Langrand (1992): Lemurs of Madagascar: An Action Plan for their Conservation. 1993-1999. – IUCN/SSC Primate Specialist Group, Gland, Switzerland.
- Mittermeier, R.A., L.H. Rakotavao, V. Randrianasolo, E.J. Sterling & D. Devitre (1987): Priorités en Matière de Conservation des Espèces de Madagascar. – International Union for Conservation of Nature (IUCN), Gland, Switzerland.
- Mittermeier, R.A., I. Tattersall, W.R. Konstant, D.M. Meyers & R.B. Mast (1994): Lemurs of Madagascar. – Conservation International, Washington, D.C.
- Nelson, R. & N. Horning (1993): AVHRR-LAC estimates of forest area in Madagascar, 1990. – *Int. J. Remote Sensing* 14:1463-1475.
- Nicoll, M.E. & O. Langrand (1989): Madagascar: Revue de la Conservation et des Aires Protégées. – World Wide Fund for Nature, Gland.
- Rabarivola, C., B. Meier, C. Langer, W. Scheffrahn & Y. Rumpler (1996): Population genetics of *Eulemur macacao macaco* (Primates: Lemuridae) on the islands of Nosy-Be and Nosy-Komba and the peninsula of Ambato (Madagascar). – *Primates* 37: 215-225.
- Richard, A.F. & S. O'Connor (1997): Degradation, transformation, and conservation: the past, present, and possible future of Madagascar's environment. – pp. 406-418 in: *Natural Change and Human Impact in Madagascar* (eds. Goodman, S.M. & B.D. Patterson). – Smithsonian Institution Press, Washington D.C.
- Saunders, D.A., R.J. Hobbs & C.R. Margules (1991): Biological consequences of ecosystem fragmentation: A review. – *Conserv. Biol.* 5: 18-32.
- Schmid, J. & R. Smolker (1998): Lemurs in the Reserve Special d'Anjanaharibe-Sud. – pp. 227-238 in: *A floral and faunal inventory of the Réserve Special d'Anjanaharibe-Sud, Madagascar: with reference to elevational variation* (ed. Goodman, S.M.). – *Fieldiana Zoology* 90. Field Museum of Natural History, Chicago.
- Smith, A.P. (1997): Deforestation, fragmentation, and reserve design in western Madagascar. – pp. 415-441 in: *Tropical Forest Remnants, Ecology, Management and Conservation of Fragmented Communities* (eds. Laurance, W.F. & R.O. Bierregaard). – University of Chicago Press, Chicago.
- Smith et al. 1997 [s.S. 1]
- Sterling, E.J. & M.G. Ramarason (1996): Rapid assessment of the primate fauna of the eastern slopes of the Réserve Naturelle d'Andringitra, Madagascar. – pp. 293-305 in: *A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: with reference to elevational variation* (ed. Goodman, S.M.). – *Fieldiana Zoology* 85.
- Storey, M., J.J. Mahoney, A.D. Saunders, R.A. Duncan, S.P. Kelly & M.F. Coffin (1995): Timing of hotspot-related volcanism and the breakup of Madagascar and India. – *Science* 267: 852-855.
- Tattersall, I. (1982): The primates of Madagascar. – Columbia University Press, New York.

- Tomiuk, J., L. Bachmann, M. Leipholdt, S. Atsalis, P.M. Kappeler, J. Schmid & J.U. Ganzhorn (1998): The impact of genetics on the conservation of Malagasy lemur species. – *Folia Primatol.* (suppl. 1) 69: 121-126.
- Turner, I. M. (1996): Species loss in fragments of tropical rain forest: a review of the evidence. – *J. Appl. Ecol.* 33: 200-219.
- Whitesides, G.H., J.F. Oates, S.M. Green & R.P. Kluberanz (1988): Estimating primate densities from transects in a West African rain forest: a comparison of techniques. – *J. Anim. Ecol.* 57: 345-367.

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Fragmentation effects on reptile and amphibian diversity in the littoral forest of southeastern Madagascar

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Abstract: QMM (QIT Madagascar Minerals), a Malagasy company owned by QIT-Fer and Titane Inc. (subsidiary of Rio Tinto plc, UK) and the State of Madagascar intend to exploit deposits of titanium dioxide principally in the form of ilmenite minerals near Tolagnaro (Fort Dauphin) in southeastern Madagascar. Most of the proposed mining area consists of highly degraded ecosystems, but some areas include wetlands and some of the remaining littoral forest of Madagascar. Conservation zones will be established and the mined areas will be rehabilitated progressively after exploitation. In order to assess possible effects of mining, and to arrive at a better understanding of the size and number of conservation zones required to preserve representative components of this ecosystem, a series of intensive impact studies have been carried out over the last few years. The present paper concentrates on the occurrence of reptile and amphibian species in differently sized fragments of the littoral forest. According to the present results the species numbers decline substantially in fragments smaller than 200 – 300 ha. Extinction with declining fragment size is non-random. Therefore a series of small fragments does not provide the biodiversity found in one or a few large fragments.

Key words: Fragmentation, reptiles, amphibians, littoral forest, Madagascar

Introduction

Despite its famous biodiversity and high degree of endemism, there have been surprisingly few studies on the effects of fragmentation on the fauna of Madagascar (Langrand & Wilmé 1997, Ganzhorn et al. 2000, Andrianarimisa et al. in press, Goodman & Rakotondravony in press). In particular, effects of habitat fragmentation on the herpetofauna are unknown. Reptiles and amphibians are well suited for analysing fragmentation effects because of their high diversity (320 species of reptiles and at least 200 species of amphibians) and their specific habitat requirements. In addition, 95% of Madagascar's reptile species and 99% of the amphibian species are endemic to the island (Blanc 1985, Blommers-Schlösser & Blanc 1991, Glaw & Vences 1994, Raxworthy & Nussbaum 1997). Due to their specific habitat requirements, herps are probably among the most suitable taxa to monitor human-induced or ecological changes which take place everywhere in Madagascar, and in the southeastern region (Anosy) in particular.

The remaining forests of Madagascar are subject to a diverse range of threats (Green & Sussman 1990, Gade 1996, Smith 1997). The lowland rain forest has been classified as one of the most threatened vegetation zones on Madagascar (Ganzhorn et al. 1997). Vast areas have already been cleared, particularly on the coastal plain, and only a small fraction of the original cover remains (Du Puy & Moat 1996). The

vulnerability due to successive attacks by man is exemplified by the forests of Anosy in southeastern Madagascar. At the beginning of the century some 60% of the region was forested. Now, forest cover has become highly fragmented and decreased to about 40% (Rakotoarisoa & Wright 1997). Extensive grasslands are important barriers between the large block of the remaining humid forest stretching along the eastern escarpment and the littoral forest on the coastal plain. In addition, the littoral forest has been broken up by people into more than a hundred fragments. The most important causes of the degradation and fragmentation of littoral forest are charcoal production, timber harvesting, grazing, and grass fires.

To save this type of habitat, QIT Madagascar Minerals established a conservation and rehabilitation program. The goal of this program is to define an ecological management plan for the flora and fauna of the coastal plain during and after mining. In order to achieve this goal, the present study addressed the following questions:

1. What are the effects of habitat fragmentation and degradation on the reptile and amphibian communities?
2. Which species occur within the project exploration zone that might be at risk of extinction or become vulnerable because of fragmentation?
3. What is the minimum size of fragments that might allow persistence of the native herpetofauna until the Conservation/Rehabilitation Program of QMM becomes effective?

Study sites and methods

The littoral forests of Mandena and Sainte Luce were selected as study sites (fig.1). Though they are part of the lowland rainforest of Madagascar's Eastern Domain, the southeastern forests growing on coastal sands are considered a distinct phytogeographic unit (Lowry & Faber-Langendoen 1991). Canopy height is 10 to 15 m, the diameter at breast height (dbh) of the largest emergent trees is generally less than 50 cm (Goodman et al. 1997). Littoral forest appears to be composed of rather dense stands of short evergreen arborescents with stiff, rounded leaves, many of which are covered with a waxy cuticle. Annual precipitation exceeds 1000 mm per year (Goodman et al. 1997). The species composition of sites in the nearby Réserve Naturelle Intégrale (RNI) d'Andohahela (63 100 ha +) was used for comparison since that might reflect the species composition of the littoral forest before fragmentation (Nussbaum et al. 1999). This comparison may not be legitimate as the coastal forests grow on poor sandy soil while the forest of Andohahela grows on lateritic soils (Goodman et al. 1997, Goodman 1999). Nevertheless, this is the best comparable database available for the time being.

Surveys were carried out in three phases:

- (1) fifteen sites of lowland and mid-altitude rainforest were surveyed between August and December 1989 and between September 1990 and January 1991;
- (2) littoral forest was surveyed by QIT in 1998/99;
- (3) to complete the regional biodiversity inventory, surveys were also undertaken in many humid and dry forest sites in the Tolagnaro region. This field work was done between 1989 and 1998 by various researchers (Creighton 1992, Ramanamanjato 1993, Raselimanana 1993, Nussbaum & Raxworthy 1994, Raxworthy & Nussbaum 1996, 1997, Nussbaum et al. 1999).

Table 1: Species list and distribution within fragments

S = Sainte Luce; M = Mandena; for the analysis of herpetofauna preference, we used the following broad categories (Goodman et al. 1997) :

Habitat: Forest (F)– species restricted to continuous tracts of disturbed or intact forest; generalist (G) – species that use forest and open habitats; Aquatic (A) – species that are found in wetland habitats in littoral zone only (excluding the sea). Lifestyle: T = terrestrial; A = arboreal. Activity: N = nocturnal; D = diurnal ; C = crepuscular; U = unknown

Species / Fragment label	S9	M15	S17	M3	S1/2	S7	S8	M4	M5	M6	M7	Habi- tat	Life style	Acti- vity
Size (ha)	457	295	244	221	212	206	191	41	28	20	10			
Amphibians														
<i>Ptychadena mascareniens</i> .	1	1		1	1	1	1	1	1	1	1	G	T	C
<i>Heterixalus boettgeri</i>	1	1	1	1		1	1	1	1	1		G	A	C
<i>Mantidactylus domerguei</i>	1	1	1	1	1	1	1	1	1			G	T	C
<i>Mantidactylus ulcerosus</i>	1	1		1	1	1	1	1	1	1		G	T	C
<i>Mantidactylus betsileanus</i>	1	1	1	1	1	1	1	1				G	T	C
<i>Mantidactyl. bicalcaratus</i>	1	1	1	1	1	1	1					F	A	D
<i>Mantidactyl. depressiceps</i>	1	1	1	1	1	1	1					F	A	C
<i>Mantidactylus punctatus</i>	1	1	1	1	1	1	1					F	A	C
<i>Mantidactylus n. sp. 1</i>	1	1	1	1	1	1	1					F	T	C
<i>Anodonthyla boulengeri</i>	1	1		1		1		1				F	A	C
<i>Plethodontohyla bipunct.</i>	1	1	1	1	1	1						F	T	C
<i>Plethodontohyla notosticta</i>	1	1	1	1	1							F	A	C
<i>Stumpffia tridactyla</i>	1	1	1	1	1							F	T	C
<i>Aglyptodactyl. madagasca.</i>	1	1	1	1								F	T	C
<i>Mantidactylus biporus</i>	1	1		1								G	T	C
<i>Plethodontohyla alluaudi</i>	1	1	1									F	T	U
<i>Boophis opisthodon</i>	1	1		1								G	A	N
<i>Mantidactylus majori</i>	1											F	T	C
<i>Scaphiophryne calcaratus</i>		1										F	T	C
<i>Boophis madagascariensis</i>	1											F	A	N
<i>Paradoxophyla palmata</i>	1											F	T	U
Reptiles														
<i>Mabuya elegans</i>	1	1	1	1	1	1	1	1	1	1	1	G	T	D
<i>Mimophis mahfalensis</i>	1	1	1	1	1	1	1	1	1	1	1	G	T	D
<i>Hemidactylus mercatorius</i>	1	1	1	1	1	1	1	1	1	1	1	G	A	N
<i>Phelsuma modesta</i>	1	1	1	1	1	1	1	1	1	1	1	G	A	D
<i>Furcifer lateralis</i>	1	1		1	1	1	1	1	1	1	1	G	A	D
<i>Furcifer oustaleti</i>	1	1	1	1	1	1	1	1	1	1		G	A	D
<i>Liopholidophis lateralis</i>	1	1	1	1	1	1	1	1	1	1		G	T	D
<i>Mabuya gravenhorsti</i>	1	1	1	1	1	1	1	1	1	1		G	T	D
<i>Madagascarophis colubri.</i>	1	1	1	1	1	1	1	1	1	1		G	T	N
<i>Phelsuma lineata</i>	1	1	1	1	1	1	1	1	1	1		G	A	D
<i>Amphigloss. melanopleura</i>	1	1	1	1	1	1	1	1	1	1		F	T	D
<i>Geckolepis maculata</i>	1	1	1	1	1	1	1	1	1			F	A	N
<i>Phelsuma quadriocellata</i>	1	1	1	1	1	1	1	1	1			F	A	D
<i>Liophidium torquatus</i>	1	1		1			1	1	1			F	T	D
<i>Lygodactylus tolampyae</i>		1		1				1	1			F	A	D
<i>Typhlops arenarius</i>		1		1					1			F	T	U
<i>Amphiglossus macrocercus</i>	1	1	1	1	1	1	1	1				F	T	D
<i>Ithycyphus oursi</i>		1		1	1		1	1	1			F	A	D
<i>Amphiglossus ornateps</i>	1	1	1	1		1	1					F	T	D
<i>Boa dumerili</i>	1	1	1	1	1							G	T	N
<i>Boa manditra</i>	1	1	1	1								F	A	N
<i>Leioheterodon madagasc.</i>	1	1	1	1								G	T	D
<i>Liophidium rhodogaster</i>	1	1	1			1						F	T	D
<i>Liophidium vaillanti</i>		1		1					1			G	T	D
<i>Lycodryas gaimardi</i>	1		1		1							F	A	N
<i>Amphiglossus melanurus</i>	1		1									F	T	D
<i>Langaha madagascariensis</i>		1		1								F	A	U
<i>Phelsuma antanosy</i>					1	1	1					F	A	D

continued

Species / Fragment label	S9	M15 /16	S17	M3	S1/2	S7	S8	M4	M5	M6	M7	Habi- tat	Life style	Acti- vity
Size (ha)	457	295	244	221	212	206	191	41	28	20	10			
<i>Pseudoxyrhopus kely</i>		1	1	1								F	T	N
<i>Amphiglossus astrolabi</i>	1	1										A	T	U
<i>Brookesia nasus</i>	1											F	A	D
<i>Calumma nasuta</i>	1											F	A	D
<i>Ithyocyphus goudoti</i>	1		1									F	A	D
<i>Liopholidophis stumpffi</i>	1											F	T	D
<i>Liopholidophis sexlineatus</i>		1										F	T	D
<i>Zonosaurus aenus</i>			1									G	T	D
<i>Zonosaurus maximus</i>		1	1									G	T	D
<i>Lycodryas arctifasciatus</i>	1											F	A	N
<i>Lycodryas betsileanus</i>	1											F	A	N
<i>Lygodactylus miops</i>	1											F	A	D
<i>Uroplatus sikorae</i>	1											F	A	N
Total number of species	51	47	36	41	29	28	27	24	22	12	6			
No. of generalist species	29	21	16	20	15	15	15	15	15	11	6			
No. of forest + marsh- dependent species	31+1	25+1	20	21	14	13	12	9	7	1	0			
Proportion of generalist species	37%	45%	44%	49%	52%	54%	56%	62%	78%	92%	100%			

The size of each fragment, shown in table 1, was defined using a point-count grid of 0.1 ha. Eleven fragments between 10 and 457 ha were selected for the present analysis. Selected fragments had regularly shaped edges whenever possible. Fragments were separated by grassland, bare sand, or denuded marshes. Most of the fragments had been isolated for at least 50 years.

Table 2: Survey efforts

MD = man-days spent at each fragment; DH = diurnal search hours; NH = nocturnal search hours; DF = drift fence (pit fall trap days)

Year	Site	MD	DH	NH	DF
1989/90	S9	22	78	16	1110
1998/99	S9	36	116	30	144
1989/90	M15/16/20	25,5	78	10	915
1998/99	M15/16/20	64	256	16	1232
1989/90	S17	7	25	8	0
1998/99	S17	12	72	10	144
1998/99	M3	21	28	14	231
1989/90	S1/2	32	128	32	319
1989/90	S7	1	6	0	0
1998/99	S7	7	14		231
1989/90	S8	4	12	0	0
1998/99	S8	2	8	0	144
1998/99	M4	21	15	12	144
1998/99	M5	21	15	8	144
1998/99	M6	21	15	8	144
1998/99	M7	21	15	8	0

Survey methods include pitfall traps and direct searching (Ramanamanjato 1993; Raselimanana 1993). Direct searching included walking of transects during the day and at night. Possible refuges were excavated with a stump ripper. Pitfall traps consisted of 15 l buckets that were placed in the ground at 10 m intervals along 100 m drift fences. Two to six drift fences were erected in each fragment and monitored daily for three to ten days depending on fragment size. The total sampling effort and pitfall traps are summarized in table 2.

Vouchers and reference specimens were collected for taxonomic identification. For each specimen, date and time of capture, activity, locality, microhabitat and biotope were collected.

Deviations of species composition in different fragments from random assemblies of species were assessed by using the program "Nestcalc; Nestedness Calculator" provided by Atmar and Patterson (1993).

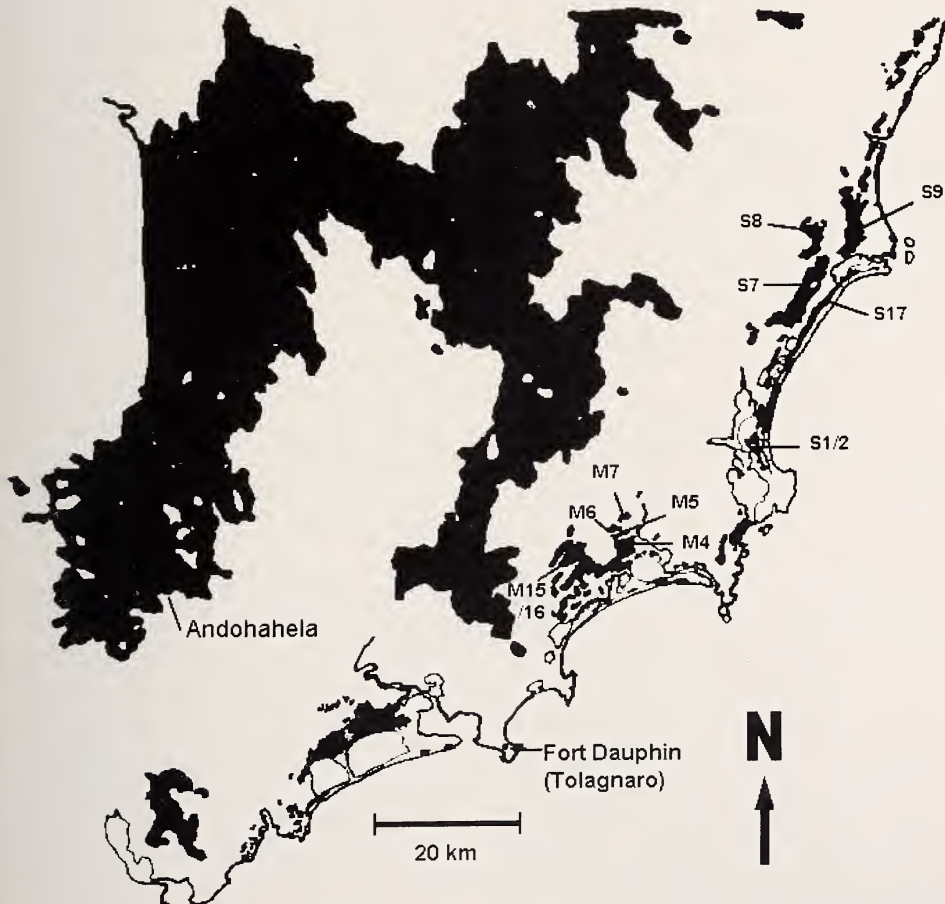


Fig.1: Location of study sites; forest areas marked in black

Results and discussion

General results

A total of 296.5 man-days of sampling effort were accumulated in the study, 866 diurnal search hours and 164 search hours at night. A total of 4902 drift fence/pitfall trap-days were accrued.

Within the 11 littoral forest fragments, a total of 83 species of reptile and amphibian were recorded. Aquatic and grassland specialist species found only outside the forest were excluded from this list. Thus the final species/area matrix used for this analysis included 62 species (41 reptiles, 21 amphibians) within 11 fragments (table 1). In the large control area of the RNI d'Andohahela, 77 reptile and amphibian species had been recorded (Nussbaum et al. 1999). Apart from the large control area, most species were found in the forest fragments S9 and in M15/16.

According to fig.2, the number of amphibian species seems to decline monotonically with decreasing fragment size, while the number of reptile species seems to decline discontinuously, with a dramatic drop in fragments smaller than around 200 ha, followed by a stabilization, then a final drop at around 50 ha.

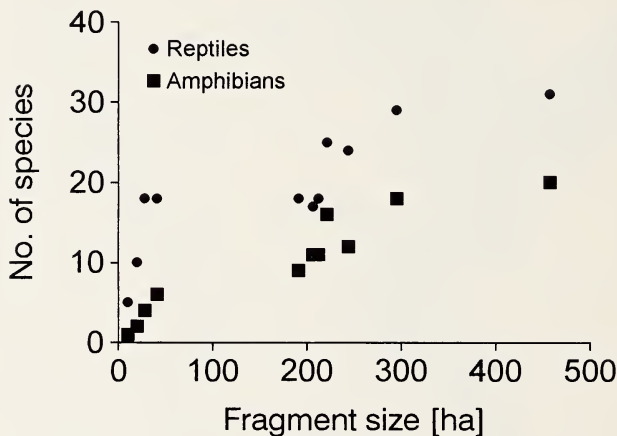


Fig.2: Species – area relationships between the number of reptile and amphibian species and fragment size in the littoral forests of southern Madagascar

The presence/absence matrix of species in different fragments deviates significantly from random species assemblages (table 1). The Nestedness Calculator Program (Atmar & Patterson 1993) assigns a temperature of 5.79° (see also Patterson & Atmar 2000, this volume) to the amphibian assemblages and 13.78° to the reptile assemblages of the 11 fragments of littoral forest. The temperature for the presence/absence pattern of the combined reptile and amphibian species assemblages is 12.11°. Random assemblages, based on 1000 simulations would have temperatures (\pm standard deviation) of $53.23^\circ \pm 6.41^\circ$, $57.47^\circ \pm 4.87^\circ$, and $59.52^\circ \pm 3.98^\circ$ respectively. Thus, the assemblages of all three groups deviate from random assemblages ($p < 0.001$ in all cases) and are consistent with nested patterns.

Vulnerability and life history characteristics

The effects of fragmentation can be seen at several levels of biological organization. At the species level, Mladenoff (1997) describes three possibilities how a given species can persist in a highly fragmented landscape. First, a species might survive or even thrive in the matrix of human land use; second, species with small home-ranges or otherwise modest area requirements might survive by maintaining viable populations within individual habitat fragments; third, highly mobile species might integrate several patches of suitable habitat, either into individual home-ranges or by exchanging individuals between subpopulations. In the littoral forest, the grassland between patches constitutes an important barrier for forest-dwelling species. This is illustrated by the fact that the decline in reptile and amphibian species seen in fig.2 is paralleled by a shift in the representation of forest-dependent species. The proportion of forest-dependent species decreased from 67% in the 457 ha fragment to 0% in the 10 ha fragment (fig.3). In the smallest fragment (10 ha) only five species of reptile and one species of amphibian were recorded during the survey work. All of them are also found in degraded forests and open areas. The complete lack of forest-dependent species in the 10 ha fragment indicates that a block of forest of this size is either unsuitable for maintaining populations of herpetological species that are large enough to survive for any length of time, or that a block of this size is not perceived as "forest" any more by the forest-dependent herpetological species. Thus, the degree of vulnerability of a given species due to forest fragmentation is likely to be related to its tolerance to habitat change and its capability to use or to bridge the new anthropogenic matrix around the remaining forest fragments (Laurance 1991, Gascon & Lovejoy 1998).

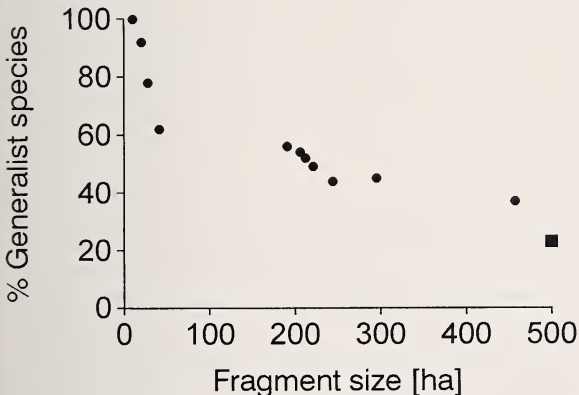


Fig. 3. Percentage of generalist reptile and amphibian species in herpetological communities in littoral forests of different size. The square represents the percentage of generalist species in the large forest (63 000 ha +) of the Réserve Naturelle Intégrale d'Andohahela (Parcel 1).

Among the categories of species predicted to be most vulnerable are the following: (1) naturally rare species: species with limited or patchy geographic distributions and species with low population densities; (2) wide-ranging species: animals requiring distinct habitats for different phases of their life cycle, such as amphibians, are also vulnerable to barriers; (3) non-vagile species: species with poor dispersal abilities that may not travel far from where they were born, or may be stopped by barriers; (4) species with low fecundity; (5) species with short life

cycles; (6) species depending on patchy or unpredictable resources or species that have highly variable population sizes for other reasons; (7) ground-nesters: nesting on or near the ground is another life history trait that seems ill suited to the ecological conditions in fragmented landscapes; (8) large patch or interior species: some species are absent from small patches with little or no true interior habitat; (9) species vulnerable to human exploitation or persecution, such as snakes and frogs that might be killed on sight (for a review see Noss & Csuti 1997).

Applying these criteria for vulnerability listed above to the herpetofauna of the littoral forest in the Fort Dauphin region, the following species might be at risk of extinction in the future.

Two forest-dwelling species (*Phelsuma antanosy* and *Pseudoxyrhopus kely*) that have a very restricted range of distribution and are presumed to be endemic to the littoral forest. Both are found only in very specific microhabitats. *Phelsuma antanosy* was discovered during the 1990/91 field study at three localities: Petriky (a forest west of Fort Dauphin, not considered here), Sainte Luce S1-S2, S7, and S8. Later, another population was discovered at Ambatororongorongo, a transitional forest about 4-5 km west of Petriky. The species seems to depend on specific palms where they lay their eggs. The exploitation of *Pandanus* and the endemic palm *Dypsis saintelucei* affect the population directly or indirectly and constitute a possible cause of extinction (Ramanamanjato & MacIntyre unpubl.). In addition, both species are only found in primary forest with a closed canopy. Between 1990 and 1994, Petriky forest was considerably reduced in size and the population of *P. antanosy* disappeared from this site.

Pseudoxyrhopus kely was also discovered during the 1990-1992 field work at two sites: M3 of Mandena and S17 of Sainte Luce. Presumed to be endemic to the littoral forest, this burrowing snake seems to occur only in patches of forest above 212 ha. It was never found in smaller fragments or in degraded forests. All of the five individuals encountered so far were seen in closed canopy forest, either under logs or after entering the pitfall traps. This species might be threatened by disruption of the closed canopy. Thus both species belong to the first categories of species vulnerability.

Four species with specific habitat requirements might also be a matter of concern. These are *Mantidactylus punctatus*, *Mantidactylus depressiceps*, *Paradoxophyla palmata*, and *Amphiglossus astrolabi*. The two frog species *Paradoxophyla palmata* and *Mantidactylus punctatus* have specialized habitat requirements. The latter relies on streams and the former on *Pandanus* plants. *Amphiglossus astrolabi* inhabits wetlands and is classified among the "Wide-Ranging Species". However, if wetlands become isolated in a matrix of grassland or bare soil, these species will not be able to migrate between patches and are likely to go extinct.

Another 17 rain forest species could be localized only in the largest blocks of the littoral forest (M15/16 and S9) with closed canopy. They are absent in small patches with little or no true interior. Human activities continue to reduce the size of M15/16 and blocks S9 and thus increase their risk of extinction as a result of forest fragmentation. The species are: *Brookesia nasus*, *Calumma nasuta*, *Liopholidophis stumpffi*, *L. sexlineatus*, *Stenophis arctifasciatus*, *S. gaimardi*, *S. betsileanus*, *Ithyophis goudoti*, *Langaha madagascariensis*, *Boa manditra*, *B. dumerilii*,

Boophis madagascariensis, *B. opisthodon*, *Mantidactylus majori*, *Aglyptodactylus madagascariensis*, *Amphiglossus melanurus*, *Lygodactylus miops*, and *Scaphiophryne calcaratus*. Most of these species are common in the eastern rain forest, such as in the RNI d'Andohahela with 63 100 ha, in Ranomafana National Park with 40 000 ha or in Andringitra Nature Reserve with 31 160 ha (Nicoll & Langrand 1989, Raxworthy & Nussbaum 1996, Nussbaum et al. 1999). In the remaining littoral forests they are restricted to the larger fragments with closed canopy forest.

According to the present results, littoral forest fragments smaller than 200–300 ha cannot retain a substantial proportion of the original faunal biodiversity. Fragments below that size, such as M4, M5, M6, and M7, are clearly impoverished. The loss of species with declining fragment size is not random but strongly deterministic. This means that from a conservation point of view one or two large forest fragments cannot be replaced by several smaller ones. It seems crucial that the ratio of forest area to edge remains high, as many species seem to react negatively to opening of the forest canopy and to yet unspecified edge effects.

Management plan and long-term monitoring

To ensure preservation of the herpetofauna of the littoral forest the following conservation actions are suggested:

1. The few existing large blocks of littoral forest (such as S9 of Sainte Luce and M15/16 of Mandena) should be protected immediately to ensure the survival of the communities listed above.
2. Corridors should be established to link some of the smaller fragments and ultimately increase the surface area of the littoral forest blocks and to help exchange individuals between fragments. QMM is currently establishing experimental corridors with native and exotic tree species to link three small fragments (M4-M5 and M5-M6) and to define options for habitat restoration.
3. In order to be successful, we need to know more about autecological aspects and the life history of various species. Several projects addressing these issues are under way.

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References

- Andrianarimisa, A., L. Bachmann, J.U. Ganzhorn, S.M. Goodman & J. Tomiuk (in press): Effects of forest fragmentation on genetic variation in endemic understory birds in central Madagascar. – *J. Ornithol.*
- Atmar, W. & B.D. Patterson (1993): The measure of order and disorder in the distribution of species in fragmented habitats. – *Oecologia* 96: 373-382.
- Blanc, C.P. (1985): Priorités en matière de conservation des reptiles et amphibiens à Madagascar. – pp. 117-120 in: Priorités en matières de conservation des espèces à Madagascar (eds. Mittermeier, R.A., L.H. Rakotovo, V. Randrianasolo, E.J. Sterling & D. Devitre). – IUCN, Gland.
- Blommers-Schlösser, R.M. A. & C.P. Blanc (1991): Amphibiens, Faune de Madagascar Edition. Vol. 75. – Muséum national d'Histoire naturelle, Paris.
- Creighton, G.K. (1992): Madagascar Minerals Project. Environmental impact assessment. Part I: Natural resources, Appendix IV. – Lewis Environmental Consultants, Montreal.
- Du Puy, D.J. & J. Moat (1996): A refined classification of the primary vegetation of Madagascar based on the underlying geology: using GIS to map its distribution and to assess its conservation status. – pp. 205-218 in: Biogeography of Madagascar, (ed. Lourenco, W.R.). – ORSTOM, Paris.
- Gade, D.W. (1996): Deforestation and its effects in highland Madagascar. – *Mountain Research and Development* 16: 101-116.
- Ganzhorn, J.U., B. Rakotosamimanana, L. Hannah, J. Hough, L. Iyer, S. Olivieri, S. Rajaobelina, C. Rodstrom & G. Tilkin (1997): Priorities for Biodiversity Conservation in Madagascar. Primate Report 48-1. – Goltze, Göttingen.
- Ganzhorn, J.U., S.M. Goodman, J.-B. Ramanamanjato, J. Ralison, D. Rakotondravony & B. Rakotosamimanana (2000): Effects of fragmentation and assessing minimum viable populations of lemurs in Madagascar. – pp.265-272 in: Isolated vertebrate communities in the tropics (ed. Rheinwald, G.) – Bonn. zool. Monogr. 46.
- Gascon, C. & T.E. Lovejoy (1998): Ecological impacts of forest fragmentation in central Amazonia. – *Zoology* 101: 273-280.
- Glaw, F. & M. Vences (1994): Amphibians and Reptiles of Madagascar, 2nd Edition. – Eigenverlag, Köln.
- Goodman, S.M. (1999): A Floral and Faunal Inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: with reference to elevational variation. – Fieldiana: Zoology, new series. Vol. 94, Field Museum Natural History, Chicago.
- Goodman, S.M. & D. Rakotondravony (in press): The effects of forest fragmentation and isolation on mammal communities (Lipotyphla: Tenrecidae) on the Central High Plateau of Madagascar. – *J. Zool.*
- Goodman, S.M., M. Pidgeon, A.F. A. Hawkins & T.S. Schulenberg (1997): The Birds of Southeastern Madagascar. – Fieldiana: Zoology, new series. Vol. 87, Field Museum of Natural History, Chicago.

- Green, G.M. & R.W. Sussman (1990): Deforestation history of the eastern rainforest of Madagascar from satellite images. – *Science* 248: 212-215.
- Langrand, O. & L. Wilme (1997): Effects of forest fragmentation on extinction patterns of the endemic avifauna on the central high plateau of Madagascar. – pp. 280-305 in: *Natural Change and Human Impact in Madagascar*. (eds. Goodman, S.M. & B.D. Patterson). – Smithsonian Institution Press, Washington, D.C.
- Laurance, W.F. (1991): Ecological correlates of extinction proneness in Australian tropical rain forest mammals. – *Cons. Biol.* 5: 79-89.
- Lowry, P.P. II. & D. Faber-Langendoen (1991): Madagascar Minerals Project. Environmental impact assessment. Part I: Natural environment, Appendix III: Flora and vegetation study. – Lewis Environmental Consultants, Montreal.
- Mladenoff, D. J. (1997): Quantifying landscape pattern and fragmentation. – pp. 279-280 in: *Principles of Conservation Biology*, 2nd ed., (eds. Meffe, G.K., C.R. Carroll & Contr.). – Sinauer Associates, Inc. Publishers, Sunderland, MA.
- Nicoll, M. & O. Langrand (1989): Madagascar: Revue de la Conservation et des Aires Protégées. – WWF, Gland, Switzerland.
- Noss, R.F. & B. Csuti (1997): Habitat fragmentation. – pp. 269-304 in: *Principles of Conservation Biology*, 2nd ed. (eds. Meffe, G.K., C.R. Carroll & Contributors). – Sinauer Associates, Inc. Publishers, Sunderland, MA.
- Nussbaum, R.A. & C.J. Raxworthy (1994): The genus *Paragehyra* (Reptilia: Sauria: Gekkonidae) in southern Madagascar. – *J. Zool.* 232: 37-59.
- Nussbaum, R.A., C.J. Raxworthy, A.P. Raselimanana & J.-B. Ramanamanjato (1999): Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andohahelo, Madagascar. – pp. 155-173 in: *A Floral and Faunal Inventory of the Réserve Naturelle Intégrale d'Andohahelo, Madagascar: with special reference to elevational variation* (ed. Goodman, S.M.). – *Fieldiana: Zoology*, new series. Vol. 94, Field Museum of Chicago, Chicago.
- Patterson, B.D. & W. Atmar (2000): Analyzing species composition in fragments. – pp. 9-23 in: *Isolated Vertebrate communities in the tropics* (ed. Rheinwald, G.). – Bonn. zool. Monogr. 46
- Rakotoarisoa, J.A. & H.R. Wright (1997): Cultural transformations and their impacts on the environments of Madagascar. – pp. 309-330 in: *Natural Change and Human Impact in Madagascar*, (eds. Goodman, S.M. & B.D. Patterson). – Smithsonian Institution Press, Washington, D.C.
- Ramanamanjato, J.-B. (1993): Contribution à l'étude des reptiles et amphibiens de la forêt ombrophile du Sud-Est de Madagascar. – DEA Thesis. Université d'Antananarivo, Antananarivo.
- Raselimanana, A.P. (1993): Contribution à l'étude de la batrachofaune et de l'herpetofaune de zones semi arides et des zones littorales de l'extrême Sud-Est de Madagascar. – DEA Thesis. Université d'Antananarivo, Antananarivo.
- Raxworthy, C.J. & R.A. Nussbaum (1996): Patterns of endemism for terrestrial vertebrates in eastern Madagascar. – pp 369-383 in: *Biogeography of Madagascar*, (ed. Lourenco, W.R.). – ORSTOM, Paris.

- Raxworthy, C.J. & R.A. Nussbaum (1997): Biogeographic patterns of reptiles in eastern Madagascar. – pp. 124-141 in: *Natural Change and Human Impact in Madagascar*, (eds. Goodman, S.M. & B.D. Patterson). – Smithsonian Institution Press, Washington, D.C.
- Smith, A.P. (1997): Deforestation, fragmentation, and reserve design in western Madagascar. – pp. 415-441 in: *Tropical Forest Remnants, Ecology, Management and Conservation of Fragmented Communities*, (eds. Lawrence, W. & O.W. Bierregaard). – University of Chicago Press, Chicago.

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Using fossils and phylogenies to understand evolution of reptile communities on islands

E.N. Arnold

Abstract: In the Mascarene islands, discovery of relict populations and fossils, together with taxonomic revision, have enabled the endemic reptile fauna existing before reduction by human colonization to be substantially reconstructed, showing it to be one of the richest oceanic reptile assemblies, with 33 species of tortoises, lizards and snakes and a further four distinctive populations of lizards. Investigation of the history of such island communities requires phylogenies of the groups concerned. These can be used to estimate original numbers of colonizations, their geographic origin (which may be from more than one direction) and patterns of inter-island spread. They also enable adaptation to island conditions to be more securely recognised and enhance investigation of such common island phenomena as change in body size, shift in niche and adaptive radiation. Relative rates of evolution on mainlands and on different kinds of islands can also be studied and it is possible to ask whether particular island communities turn over rapidly, and why island populations are so vulnerable to incoming predators and competitors. Finally the possibility can be considered that islands are "black holes" from which mainlands are rarely if ever colonized. As well as the Mascarene islands, examples are taken from the Soqotra, Canary and Cape Verde archipelagos.

Key words: Mascarene islands, Soqotra, Cape Verde islands, Canary islands, colonization, adaptation, radiation.

Introduction

Islands and archipelagos are favourite places to study evolution. They usually have the advantages of apparently simple communities that often originated quite recently and some of the selective forces that helped mould them frequently seem evident. Yet it is also clear that what is being studied is likely to be fragmentary, or at least very different from what was present even in the recent past, for the arrival of people on previously uncolonized islands has almost always devastated their biotas. The equilibrium theory of island biogeography suggests there may also have been considerable natural change in species composition in many cases.

As the history of lineages affects how evolution and especially adaptation takes place in them, it is necessary to know as much about the past of island communities as possible and this is also important as a basis for designing conservation strategies. While history once tended to be relatively neglected in island studies, the past few decades have seen greater interest and a number of approaches have been employed to obtain a fuller understanding of island communities. These include:

1. searching islands and archipelagos as thoroughly as possible for relict populations of once more widespread forms;
2. revising current taxonomies, often exposing unknown taxa;

3. looking for fossils;
4. using old accounts and old museum specimens;
5. using phylogenies to reconstruct clade history.

Some of these approaches will be illustrated using examples from West Indian Ocean and North Atlantic reptile communities.

Reconstructing the reptile fauna of the Mascarene islands

The Mascarene islands comprise, from west to east, the islands of Réunion, Mauritius and Rodrigues and lie some 500 km east of Madagascar. They are classic volcanic oceanic islands and had no previous connexion with other areas of land. Some fifty years ago, their known living endemic reptile fauna was quite modest, consisting of perhaps eight recognised species. Since that time additional relict but surviving species have been discovered. These include three species of night gecko on Mauritius, *Nactus serpensinsula* (Loveridge, 1951), *N. durrelli* Arnold & Jones, 1995 and *N. coindemerensis* Bullock et al., 1985, two kinds of day gecko on Réunion, *Phelsuma borbonica* Mertens, 1966 and *P. inexpectata* Mertens, 1966, a new Slit-eared skink, *Gongylomorphus fontenayi* Vinson, 1974 and additional distinctive populations of this species and *G. bojeri*. The majority of these forms are now confined to one or more small islets around Mauritius, most lying to the north of the main island. One of these islets, Round Island, was already known to have unique forms, including Gunther's gecko (*Phelsuma guentheri*), Telfair's skink (*Leiopisma telfairi*) and two species of bolyerine snake assigned to different genera, *Casarea dussumieri* and *Bolyeria multocarinata*. Systematic revision has also shown that the small day geckos (*Phelsuma*) of Mauritius actually consist of four species (Mertens 1963, 1966, 1970, Austin & Arnold, in progress).

Fossils, collected mainly in the nineteenth century, confirmed historical records of a giant gecko (*Phelsuma gigas*) on Rodrigues, which disappeared in the mid-1800s, and uncovered no less than five endemic species of Mascarene giant tortoises (*Cylindraspis*). They also revealed the original presence of a giant skink (*Leiopisma mauritiana*) on Mauritius that weighed perhaps ten times as much as its surviving sympatric congener, *L. telfairi*. More recent fossil discoveries include species of *Nactus* and *Leiopisma* from Réunion (Arnold and Bour, in progress), two more *Nactus* from Rodrigues as well as two further previously unknown extinct geckos, and extensive remains of *Phelsuma edwardnewtoni*, which disappeared around 1920 (Arnold, Austin & Jones, in progress). Fossils have also been important in extending ranges and many of the relict forms now confined to islets near Mauritius turn out to have once been widely distributed on the main island (Arnold 1980). Cave deposits additionally provide evidence of recent species turnover which is certainly anthropogenic. Those in Rodrigues contain extensive remains of six recently extinct geckos, but of only one of the five gecko species that occur on the island today, confirming that the others are post-colonization introductions (Arnold, Austin, Jones, in progress).

The synthetic approach related above has increased the number of known Mascarene endemic reptile species to around 33 with two additional distinctive

Table 1: Extinct and surviving endemic reptiles of the Mascarene islands.

† - extinct, * - relict, # - distinctive populations exist.

	Réunion	Mauritius	Rodrigues
Giant tortoises			
<i>Cylindraspis</i>	<i>C. indica</i> †	<i>C. inepta</i> † <i>C. triserrata</i> †	<i>C. vosmaeri</i> † <i>C. peltastes</i> †
Day geckos			
<i>Phelsuma</i>	<i>P. borbonica</i> # <i>P. inexpectata</i> *	<i>P. guentheri</i> * <i>P. cepediana</i> # <i>P. ornata</i> <i>P. guimbeau</i> <i>P. roseogularis</i>	<i>P. gigas</i> † <i>P. edwardnewtoni</i> †
Night geckos			
<i>Nactus</i>	<i>N. sp.</i> †	<i>N. serpensinsula</i> * <i>N. durrelli</i> * <i>N. coindemerensis</i> *	<i>N. sp. A</i> † <i>N. sp. B</i> †
Waif gecko			
<i>Lepidodactylus</i>			<i>L. lugubris</i>
Unidentified geckos			
			Two species †
Mascarene skinks			
<i>Leiopisma</i>	<i>L. sp.</i> †	<i>L. telfairi</i> * <i>L. mauritiana</i> †	
Slit-eared skinks			
<i>Gongylomorphus</i>	<i>G. borbonica</i> †	<i>G. bojeri</i> * # <i>G. fontenayi</i> * #	
Shore skink			
<i>Cryptoblepharus</i>		<i>C. boutoni</i>	
Bolyerine snakes			
<i>Casarea</i>		<i>C. dussumieri</i> *	
<i>Bolyeria</i>		<i>B. multocarinata</i> * / † ?	

populations of *Gongylomorphus* and two of *Phelsuma* (table 1). This makes them one of the richest known oceanic island reptile faunas. Of the 33 species, at least 15 (46%) are extinct, 11 (33%) reduced to small relicts and only seven (21%) retain substantial ranges.

Fossil remains are also useful in reconstructing life-modes of extinct forms. The ratio of stable carbon isotopes, C_{12}/C_{13} , in the bones of herbivores reflects the kinds of plants that they ate and it is clear from this that the extinct giant tortoise, *Dipsochelys grandidieri*, from Madagascar consumed a much higher proportion of grass than other species in the southwest Indian Ocean (Burleigh & Arnold 1986). It has been suggested that the fossil giant Mauritian skink was arboreal and vegetarian, like another very large skink, *Corucia zebrata*, of the Solomon islands, but its teeth are shaped very like the surviving *L. telfairi*, an omnivore, and lack vegetarian specialisation. The teeth are also scored and pitted by grit, a common

phenomenon in forms that spend a lot of time on the ground but usually much less obvious in ones that climb extensively.

Old material in museums has also been important in understanding the Mascarene herpetofauna, especially as they are potential sources of DNA for molecular studies and sometimes this is important in identifying them. The type of the tortoise named as *Testudo indica* is a shell believed to have been in Paris since the 1670s (Vaillant 1899), and that constituting the type of *T. graii* has been there since at least the early nineteenth century. Although both these shells were thought to come from the Mascarenes, this was unconfirmed as was their specific island of origin. Mitochondrial DNA from these shells has recently been compared with that from fossil bones collected on particular islands and it is clear that both came from the extinct Réunion species (Austin, Arnold, Bour, in progress). This identification helps resolve nomenclature and it is now clear that the name *Cylindraspis indica* should be applied to the Réunion form. Allocation of these shells also provides more information about the populations concerned. Unlike fossils, such specimens may retain full shell proportions, colouring and surface growth rings, the latter providing some evidence of growth rate, hatching size and consequently egg-size in these extinct animals.

Old museum specimens have also proved a useful source of DNA in other cases. Sequence extracted from specimens collected in 1931 of the extinct large lacertid lizard, *Gallotia simonyi*, of the Roques Salmor in the Canary islands is identical with that of *G. s. machadoi* on neighbouring Hierro island, validating the recent reintroduction of lizards to the Roques from this source (Carranza et al. 1999). Similarly, 110 year old museum material recently provided DNA elucidating the relationships of the enigmatic giant skink, *Macroscincus coctei* of the Cape Verde islands (Carranza & Arnold, in progress).

Aldabra atoll, an example of longer term historical change

Aldabra atoll, which lies about 420 km northwest of the northern tip of Madagascar, has a small contemporary reptile fauna consisting of giant tortoises (*Dipsochelys*) and three lizards widespread in surrounding areas: the geckos *Hemidactylus mercatorius* and *Phelsuma abbotti*, and the skink *Cryptablepharus boutoni*. Fossils are available from two horizons, the Bassin Cabri calcarinites, about 500 000 years old, and cavity fillings in the Aldabra limestone at Point Hodoul less than 100 000 years old (Braithwaite et al. 1973, Taylor et al. 1979). Giant tortoises, crocodiles and iguanids (*Oplurus*) occur at Bassin Cabri and also at Point Hodoul where five more lizard species are found that do not occur on the island today: geckos of the genera *Paroedura*, *Geckolepis* and *Phelsuma*, and two skinks, an *Amphiglossus* and *Mabuya* cf. *maculilabris* (Arnold 1976). It is probable that Aldabra was completely submerged after the Bassin Cabri calcarinites were laid down and again after the Point Hodoul deposits (Braithwaite et al. 1973, Taylor et al. 1979). If so, giant tortoises must have colonized the atoll at least three times, and crocodiles and iguanians at least twice each. The atoll had substantial faunal change but submergence means there was no continuity between the three horizons for which information is available.

Uses of phylogenies

The recent availability of estimates of phylogeny for many groups permits speculations about the history of island communities to be tested more rigorously and some of their uses in this context will be outlined here.

Numbers of colonizations

Knowledge of phylogeny permits the minimum number of colonizations of islands to be estimated. Essentially, if an island taxon has its closest relatives in an assumed source area, rather than on the island itself, it is likely to represent an independent colonization of the island. Cases where island forms have subsequently invaded other areas may complicate such inference but these seem to be rare. On the basis of this approach, the Mascarenes may have evolved their present fauna from just eight original invaders: single ancestral species of the endemic *Cylindraspis*, *Nactus*, *Phelsuma*, *Lepidodactylus*, *Gongylomorphus*, *Leiopisma* and *Cryptoblepharus* and a single ancestor of the two genera of bolyerine snakes. As on Aldabra, fossils may increase the known number of colonizations, both by showing that more taxa actually arrived and that some of them arrived more than once.

Mainland origins of colonizations

Phylogenetic information often permits the geographic origin of island populations to be assessed. Origin is most certain where an island taxon has its sister group in a particular geographic area in which successively deeper branches of the clade concerned also occur. It is often assumed that the closest land mass to an island or archipelago is the most likely source area for colonists and this is indeed often the case. Aldabra clearly gained its successive faunas from Madagascar or the Comores islands or both. Similarly the Galápagos got its biota from nearby South America, and the Canary islands from northwest Africa. In contrast the reptile fauna of the Mascarenes came from two different directions. The closest land mass is Madagascar, about 500km away to the east, and phylogeny suggests that *Phelsuma* and *Gongylomorphus* reached the islands from this direction. Other taxa are members of more eastern groups based in tropical Australasia and adjoining areas, including *Nactus*, *Lepidodactylus*, *Cryptoblepharus*, and *Leiopisma* which is a member of the Australasian and Melanesian eugongylid radiation of skinks (Greer 1990); the bolyerine snakes may also have had an eastern origin. All these forms must have made journeys of at least 4500 km to the Mascarenes, a greater distance than that separating the Hawaiian archipelago (usually considered the most isolated in the world) from the nearest mainland. Such huge journeys are less surprising when it is realised that they are greatly facilitated by dispersal agents such as currents and winds. The Equatorial current runs westwards towards the Mascarenes from tropical Australasia and is capable of transporting natural rafts that might carry propagules; the Southeast Trade winds provide additional westward impetus. Such factors are important in other cases of long-distance colonization. A northward current passing Madagascar probably brought many propagules from there to Aldabra and it is estimated that they could have made the 420 km journey

in 3-9 days (Taylor et al. 1979). Primarily North African *Tarentola* geckos travelled 1400 km between the Canary and Cape Verde islands on the Canary current (Joger 1984, Carranza & Arnold, submitted). This runs at about 14-20 km a day (Guppy 1917), so the journey may have taken about ten weeks. *Tarentola* also reached Cuba, presumably via the Northern Equatorial current, a distance of over 6000 km (Carranza & Arnold, submitted). Sometimes journeys take place against prevailing dispersal agents, for instance those made between Madagascar and the Mascarenes. These may have been promoted by short-term cyclonic storms the tracks of which sometimes cross both areas. Certainly cyclones can move reptiles very rapidly at times, often over substantial distances (Townsend 1936, Censky et al. 1998).

Patterns of inter-island spread

Not only do taxa reach archipelagos, they also spread through them. The number of possible patterns of colonization increases non-linearly with the number of islands involved. If simple sequences are considered, with spread from one island to another, the number of possibilities for n islands is n factorial $n! = 1.2.3. \dots (n-1)n$, that is six possibilities for three islands, twelve for four and 604800 for ten. If branching sequences are included, the number may be $n \cdot n-1$, which is six for three islands, 64 for four and a billion for ten! Even this does not exhaust possibilities, for it ignores situations where sequences branch and there may be different orders of colonization. For three islands there are then twelve possibilities and 144 for four islands. Numbers increase yet again if particular islands are colonized more than once, something that is often apparent if speciation has taken place.

Fortunately, a robust phylogeny of the island populations involved radically reduces the number of possibilities, although even then different colonization sequences are possible. For instance a phylogeny of four island populations, 1(2 (3,4)), could represent sequential colonization from 1, that is 1 -> 2 -> 3 -> 4 or 1 -> 2 -> 4 -> 3, or repeated colonization of the other islands from 3 or 4, for instance: 4 -> 1, 4 -> 2, 4 -> 3.

Various approaches are helpful for choosing between possibilities, one being distance parsimony where the colonization pattern involving the shortest route is favoured. Another is journey parsimony where the sequence involving the fewest inter-island journeys is accepted. In practice, this can be accomplished using the MacClade program (Maddison & Maddison 1996) and scoring different islands or island groups as separate states of a single character.

Dispersal agents are also important in understanding colonization sequences. For instance, the Canary current not only brought *Tarentola* to the Cape Verde islands but also spread these geckos southward through the archipelago and the same may be true in the Canaries (Carranza & Arnold, submitted).

Dispersal ability of taxa also affects pattern of spread. If possible ability is best judged in a particular case by the performance of a range of relatives, as sometimes a particular taxon may lose dispersal ability once it has reached an island. Some groups like *Tarentola* clearly disperse well having made numerous, often long journeys. Others like lacertid lizards have more restricted abilities. It is not surprising therefore that Canary island lacertids (*Gallotia*) have not emulated

Tarentola in reaching the Cape Verdes but have made only modest journeys within the Canaries, each of a 100 km or less. These journeys run successively westwards along the archipelago traversing the prevailing winds and currents. Restricted dispersal ability together with island topology has dictated that these lizards are moved by rare storms rather than the prevailing dispersal agents.

Recognizing island adaptations

The distinctive features of many island species are often assumed to be adaptations by natural selection to the island situation, but phylogenies show this is not always the case. For instance Soqatra and its satellite islands, off the Horn of Africa, has several endemic species of Semaphore gecko (*Pristurus*) that look at first sight like an adaptive radiation. But phylogenetic analysis shows that they are not a clade and comprise a series of successive branches near the base of the main lineage of *Pristurus* and most current mainland species have evolved after them (Arnold 1990, 1993). Also, what look like distinctive features are really primitive characteristics of *Pristurus*. Soqatra is a continental island that broke away from southern Arabia in the mid-Miocene (Beydoun & Bichan 1970) and its Semaphore geckos may represent lineages and morphologies that were widespread in this area at the time, but are now otherwise extinct.

There are a number of possible indicators of island adaptation, that is where a trait has actually developed in response to insular conditions.

1. The feature concerned should actually confer performance advantage in the island selective regime, or at least be likely to do so. This is more convincing if the island situation is markedly different from that in the mainland or other area where the organisms concerned originated.
2. The feature is likely to have originated on the island concerned rather than before colonization took place.
3. The feature has developed independently in similar organisms on separate lineages that have also reached islands.

Phylogenies can be helpful here in testing points 2 and 3. They can show that features of island forms are in fact derived compared with those of their mainland relatives, rather than being conserved primitive features, and they can confirm that similar animals on different islands are members of independent lineages when this is the case.

Giant tortoises have survived in recent times only on isolated island groups. A member of the subgenus *Chelonoidis* still occurs wild on the Galápagos. *Dipsochelys* is still found on Aldabra atoll in the southwest Indian Ocean and until about 1800, was on the Seychelles. Finally the Mascarenes had the five species of the endemic genus *Cylindraspis* which finally disappeared at about the same time.

Mascarene tortoises had many distinctive features (Arnold 1979). The shell was often very thin, sometimes being only 2 mm thick in parts and weighing about a third of that of similar mainland tortoises; it also had a very small belly section, the plastron. The two shell openings where the limbs, head and tail projected were huge and there was no thickening of the shell at the borders of these openings. Some species had primitively rounded shells like most tortoises, but two had independently developed a 'saddle-back' configuration in which the front of the shell is raised so that it is as high or higher than the mid-back. All these features

were poorly developed in mainland giant tortoises when these existed and have also evolved independently to varying extents in the separate Galápagos and Seychelles and Aldabra giant tortoise lineages, suggesting that they are indeed island adaptations.

Their development is very probably related to common characteristics of oceanic islands. The island habitats of giant tortoises all lack large competing herbivores and big predators, so tortoises often attained very high densities. Leguat (1708) noted that on Rodrigues dense herds could be 100 paces across and on the small island of Aldabra there were over 150 000 animals in the 1970s (Coe et al. 1979), although numbers are now falling because food supplies have become exhausted. Such population fluctuations are likely to have been made worse at times by climatic irregularity such as that produced by El Niño.

Tortoises were consequently probably intermittently subjected to very strong intraspecific competition for food and in this situation modifying the shell had many advantages. The cost of shell maintenance and carriage was reduced and the open shell meant that animals probably could be more agile in reaching food in the rugged terrain of their often volcanic islands. The high front of saddle-back shells increased upward reach when browsing by raising the base of the neck which was also elongated. The modified shell allowed this extended neck to be housed when the head was withdrawn into it. In the Galápagos such shells occur on dry islands with sparse vegetation where their lack of streamlining does not impede movement and increased browsing range is particularly beneficial. On Mauritius and Rodrigues rounded and saddle-back species occurred sympatrically on the same islands their different browsing abilities perhaps reducing inter-specific competition (Arnold 1979).

While adaptive changes appear to have been driven by strong intraspecific competition, another common insular feature facilitated their development, namely the absence of all or most predators. Many of the changes to the shell involve dismantling the usual anti-predator devices of tortoises which were no longer needed, including a heavy rounded shell with small openings that can be blocked by armoured limbs and which have thickened edges that prevent them being enlarged by carnivores.

The large size of giant tortoises has also been considered an insular adaptation evolved as tortoises occupied the vacant large-herbivore niche on oceanic islands. But the tortoises of Madagascar, the apparent source area for the Seychelles and Aldabra populations were equally big. In at least this case, large size may have facilitated transmarine island colonization, as big tortoises float well and can carry their heads clear of the water, but it was not an adaptation to island conditions as such.

The Mauritian skink, *Leiolopisma telfairi* also appears to have reduced ancestral anti-predator mechanisms in response to strong intra-specific competition, for like giant tortoises it reaches very high densities, the population of the 1 km long Round island having been estimated at 100 000. Lizards primitively often evade predators by shedding the tail, which acts as an effective distraction for a pursuer as it often continues to move and contains a substantial proportion of the owner's valuable fat reserves. On small islands where food is frequently sparse, some lizards pull off

and eat the tails of conspecifics thereby harvesting a large part of their energy reserves. The evolutionary response to this is sometimes to decrease the fragility of the tail (Arnold 1984), so it is harder to steal, something that has happened in several island populations of Mediterranean wall lizards (Pérez-Mellado et al. 1998). The same trend is apparent in *L. telfairi* where, although the tail is breakable, it is tough and cannot be removed easily. The lizards will also often turn and defend the tail by biting if caught by it. Moreover the tail is slender and contains relatively little fat, reserves now being stored predominantly in the body.

Other Mascarene taxa have evolved very distinctive features apparently within the archipelago, but the case for their being adaptations to island conditions is not always broadly supported. As their name suggests, Slit-eared skinks (*Gongylomorphus*) have modified ear openings. These are dorsoventrally narrowed, protected by a projecting chevaux-de-frise of spines, and are closable. A strange muscle system on the snout appears to be capable of occluding the nasal passages and there are dense batteries of backwardly directed sense organs above the ear openings, along the flanks and on the thighs. These features seem almost paranoid, as if in evolutionary terms the lizards are concerned about something approaching them from behind and penetrating their body openings. An insect parasitoid that deposits eggs or carnivorous larvae in such places could be postulated, yet no such predator has been observed to date. So a case for advantage in the island situation is lacking, and as these features of *Gongylomorphus* are more or less unique, it is not possible to use independent parallel cases on other islands to infer insular adaptation.

Change in body size

This is often postulated to occur after reptiles arrive on islands, especially marked increase in size leading to insular gigantism, and phylogenies permit such cases to be tested. They show that the lacertid lizards, *Gallotia*, have indeed become the largest members of their family since their colonization of the central and western Canary islands and adoption of a vegetarian diet. The extinct Mauritian giant skink (*Leiopisma mauritiana*) also reached its large size in situ (Austin & Arnold, in progress) and the same is true of the Cape Verde giant skink (*Macroscincus coctei*) and gecko (*Tarentola gigas*) (Carranza & Arnold, in progress). However, size increase is by no means universal in island reptiles. Like at least some giant tortoises, the big *Phelsuma* of the Mascarenes may be descended from quite large colonizers (Austin & Arnold, in progress). Size has also sometimes fallen. In the Mascarenes, this appears true of one of the Rodrigues species of giant tortoise, *Cylindraspis peltastes*, of the night gecko, *Nactus coindemerensis*, and of the ancestor of a clade of six small species of *Phelsuma* in Mauritius and Réunion (Austin & Arnold, in progress). So, body size of island reptiles often changes, but not in a consistent way.

Shift in niche

Some island forms occur in ecological situations markedly different from those occupied by their mainland relatives, presumably because in the sparse communities often found on islands such situations are otherwise unoccupied and

can be exploited. For instance, there may be a shift in time of activity: *Phelsuma* is ancestrally diurnal, but *P. guentheri* of Mauritius and *P. gigas* of Rodrigues have become substantially night-active (Arnold, in press). The shifts in body size mentioned above may also reflect exploitation of new resources. In some cases there may be a general broadening of niche. This is reflected in several niche parameters of the Mauritian *Leiopisma telfairi*. This species can be active both by day and night, its diet includes both smaller animals and vegetation, and its spatial niche involves foraging on rocks and in vegetation as well as hunting on the ground, furthermore young animals occupy different habitats from adults. So a range of niche space is covered that might support a number of species in mainland environments.

Adaptive radiation

This phenomenon is often associated with islands and classical examples include the Galápagos finches, and the honey creepers (Drepanidinae) and fruit flies (*Drosophila*) of Hawaii. Yet adaptive radiation is not extensive in some archipelagos and insular taxonomic groups. It is inevitably associated with substantial speciation, so its extent in an archipelago can be partly assessed from the ratio of the number of species known to be present in a taxon to the minimum number of initial colonists. In the case of Mascarene reptiles (33 species and eight colonizations), the ratio is 4.1:1 (compared with about 2.6:1 and 3.3:1 in the Canaries and Cape Verdes). In Mascarene reptiles, the number of speciation events known to have occurred in particular groups varies from none, to nine in *Phelsuma*. Presumably a high general level of adaptive radiation in islands results partly from a low level of colonization compared with the diversity of the available ecological resources, but variation between individual taxa probably reflects such group specific features as the facility with which speciation occurs.

Relative rates of evolution

Phylogenies can of course often be used to recognize the mainland sister groups of island forms. As sister groups arise simultaneously and are thus the same age, it is possible to compare how much evolution has occurred in them over the same time span. In the case of oceanic islands where the island lineage enters a new habitat and the mainland one remains in more or less the same environment, it is to be expected that, initially at least, the island lineage will change faster (although in periods of global climatic change both mainlands and islands may alter radically). Certainly, greater morphological and behavioural change often does occur in oceanic island forms compared with their mainland sisters. Galápagos finches have radiated and altered far more than the South American grassquit, which probably shares an exclusive common ancestor with them (Steadman 1982). The same is true of Hawaiian honey creepers compared with their probable sister taxon, a Holarctic grosbeak. Island giant tortoises have also changed more than their likely mainland relatives (Arnold 1979).

Greater change on islands than mainlands is not always the case. As already mentioned, Semaphore geckos on Soqotra have maintained similar morphologies perhaps since the mid-Miocene, but the mainland sister group of one of them has

produced a radiation of a dozen species including forms that have altered radically, even converging on desert iguanian lizards and being active at higher temperatures than any other geckos (Arnold 1993). Similarly the worm lizard, *Pachycalamus*, of Soqatra remains monotypic and relatively primitive while its mainland sister clade has speciated and produced different morphologies.

Possibly less change in general occurs on continental islands compared with oceanic ones. They are likely to separate from mainlands with relatively large populations of at least some of the species they share with these, so founder effects may be improbable. They are also likely to begin with an established community in place, so there will be less opportunity for species to shift into empty niche space with consequent evolutionary change. Such island communities will also be protected to some extent from incoming taxa likely to affect related mainland ones and they may also sometimes be less subject to climatic change. Not all taxa on a continental island necessarily date back to its separation, for it too is subject to transmarine migration. Forms arriving by this means may be distinguishable by molecular clock data and late appearance in any fossil record the island may have.

Do island communities turn over regularly?

Species in island populations may change steadily over time, some becoming extinct and being replaced by new colonizers (MacArthur & Wilson 1967). This is certainly true for small islands and low ones subject to at least intermittent habitat loss, or even inundation like Aldabra. With larger, higher, more distant islands many taxa seem to persist over long periods, certainly long enough to undergo repeated speciation as *Phelsuma* has done in the Mascarenes, *Gallotia* in the Canaries and *Tarentola* in the Canary and the Cape Verde islands. Incorporating molecular clocks into phylogenies suggests *Gallotia* may have been in the Canaries for more than 12 My and *Tarentola* in the Cape Verdes for more than 4 My (Carranza & Arnold, submitted). Any non-anthropogenic turnover involving such groups must consequently be extremely slow.

Why are island populations so vulnerable?

Island taxa are very vulnerable to many introduced predators. Herbivorous ones destroy vegetation and thus habitats. People were among the main factors in reducing the Mascarene tortoises by direct exploitation (Bour & North-Coombes 1988) and domestic introductions such as pigs and dogs contributed as well. Inadvertently introduced animals were also important, especially those often associated with people such as rats, but also more exotic introductions like the Indian snake, *Lycodon aulicus capucinus* which may well have exterminated Slit-eared skinks on Réunion and most of Mauritius in the 1800s (Jones 1993).

Exotic competitors may also be important in loss of native forms. In the Mascarenes, endemic night geckos, *Nactus*, have probably been exterminated on some islands by the introduced *Hemidactylus frenatus* which has about the same range of body size (Arnold & Jones 1995). *Nactus* are now known to occur on just five off-shore islands while eight islands, often very close to these, are occupied by introduced *Hemidactylus* geckos. The probability that the allopatric dove-tailed distributions of these two genera is due to chance is <0.001 (exact χ^2 test). This

pattern cannot simply be a result of mutual competitive exclusion by the two genera as they colonized the islands, because *Hemidactylus* appears to be a very recent anthropogenic introduction while *Nactus* has been in the Mascarenes long enough to produce a radiation of about six species. *Hemidactylus* appears only to occur on islands that have been inhabited by people and, on some of these, recent fossils show that *Nactus* was originally present. Nor is anthropogenic habitat destruction likely to be the cause of the disappearance of *Nactus* as it survives on islets where most vegetation has disappeared.

Vulnerability to incoming predators and competitors appears to be partly because island taxa have not been in contact with the enemies concerned, at least in recent evolutionary time and cannot adapt to them because on small islands endemics are often rapidly and completely exterminated before this can happen, as has been directly observed in several native birds on Guam after the introduction of the snake *Bioga irregularis* (Jaffe 1994). The problem is exacerbated because, as noted in tortoises and *Leiopisma*, anti-predator devices present when taxa reach islands are sometimes dismantled in response to intensified intraspecific competition. Although formidable and relatively large lizards, *Leiopisma* have been extirpated from nearly all of their original range apparently by rats, even though superficially similar skinks coexist with these mammals on mainlands. Presumably reduction of the tail shedding mechanism and inappropriate defence responses associated with this are the cause. More general features important in countering predators and competitors, such as speed of movement may also be attenuated in island situations. For instance locomotion in the wall lizard, *Podarcis atrata*, of the Columbretes islands off northeast Spain is markedly slower than in its congeners on the neighbouring mainland (Van Damme 1998).

Are islands black holes?

The way organisms regularly reach oceanic islands and adapt to their special conditions is impressive, but does such evolution have long-term prospects? Does the vulnerability to introduced predators and competitors characteristic of island forms prevent them from going on to colonize mainlands where such enemies naturally occur? This is in principle testable by using phylogenies to trace the total subsequent history of lineages that have colonized islands. If evolution on islands produces forms that can survive on mainlands, occasional invasions of these are to be expected and would often be reflected by paraphyly of island taxa with respect to related mainland forms. If, on the other hand, islands are like astronomical black holes, so colonizing lineages can enter but rarely if ever escape, such evidence should be lacking. In such investigations, it is necessary to ensure that failure to reach mainlands is not just a function of distance.

There is evidence that *Phelsuma* originated on Madagascar and that different lineages independently reached the Mascarenes, the Seychelles, and even the Andaman and Nicobar islands a straight-line distance of 6000km (Austin & Arnold, in progress). In none of these cases have the island forms moved significantly on to mainlands. This is even so for *P. parkeri* which occurs on Pemba island just 50km from the African mainland. Similarly *P. andamensis* is a mere 300 km from the coast of Burma, a short distance compared with that from its source area.

Obviously, many examples must be examined to test whether this phenomenon is usual.

If it is actually the island interlude that prevents insular groups invading mainlands, some cases where one mainland has been colonized from another are to be expected and indeed actually occur. Morphology indicates that several taxa present in Africa have reached tropical America by transmarine migration probably via the South Equatorial current. Included here are skinks, *Mabuya*, and gekkonids, *Lygodactylus* and *Hemidactylus* (Kluge 1969). Also the Brazilian gecko *Briba* appears to be closely related to the West African *Hemidactylus longicephalus* group, while the neotropical *Bogertia*, *Phyllopezus* and *Thecadactylus* have similarities to the African and Madagascan *Homopholis* assemblage (Russell 1975). Invasion of one archipelago from another is also known, as already noted *Tarentola* geckos have reached the Cape Verde islands from the Canaries, but does not seem very common.

Concluding remarks

Fossils and phylogenies illuminate the history of island communities, add detail to them and enable a range of hypotheses to be tested. Among other things they help reveal the very wide variety of phenomena that occur, particularly the differences between particular taxa and archipelagos. For instance, while colonizing *Anolis* in the Greater Antilles have speciated to produce a similar range of morphotypes on different islands (Losos et al. 1998), in the Mascarenes *Phelsuma* has two large species on Rodrigues, two small ones on Réunion and one large and four small species on Mauritius.

Acknowledgements

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References

- Arnold, E. N. (1976): Fossil reptiles from Aldabra atoll, Indian Ocean. – Bull. Brit. Mus. nat. Hist. (Zool.) 29: 83-116.
- Arnold, E. N. (1979): Indian Ocean giant tortoises: their systematics and island adaptations. – Phil. Trans. R. Soc. Lond. B 286: 127-145.
- Arnold E. N. (1980): Recently extinct reptile populations from Mauritius and Réunion, Indian Ocean. – J. Zool. Lond. 191: 33-47.
- Arnold, E. N. (1984): Evolutionary aspects of tail shedding in lizards and their relatives. – J. Nat. Hist. 18: 127-169.

- Arnold, E.N. (1990): Why do morphological phylogenies vary in quality? An investigation based on the comparative history of lizard clades. – *Proc. R. Soc. B* 240: 135-172.
- Arnold, E.N. (1993): Historical changes in the ecology and behaviour of semaphore geckos (*Pristurus*, Gekkonidae) and their relatives. – *J. Zool. Lond.* 229: 353-384.
- Arnold, E.N. (in press): Methods of inferring unknown aspects of organisms and the behavioral origins of bird flight. *New Perspectives on the Origins and early evolution of birds.* – New Haven: Yale University Press.
- Arnold, E.N. & C.G. Jones (1995): The night geckos of the genus *Nactus* in the Mascarene islands with a description of the distinctive population on Round Island. – *Dodo, Jersey Wildlife Preservation Trust* 30: 119-131.
- Beydoun, Z.R. & H.R. Bichan (1970): The geology of Socotra Island, Gulf of Aden. – *Q. J. Geol. Soc.* 15: 413-446.
- Bour & North-Coombes, Braithwaite, C.J.R., J.D. Taylor & W.J. Kennedy (1973): The evolution of an atoll: the depositional and erosional history of Aldabra. – *Phil. Trans. R. Soc. B* 266: 307-340.
- Bullock, D.J., E.N. Arnold & Q. Bloxham (1985): A new endemic gecko (Reptilia: Gekkonidae) from Mauritius. – *J. Zool. Lond.* 206: 591-599.
- Burleigh, R. & E.N. Arnold (1986): Age and dietary differences of recently extinct Indian Ocean tortoises (*Geochelone* s.lat.) revealed by carbon isotope analysis. – *Proc. R. Soc. Lond. B* 227: 137-144.
- Carranza, S. & E.N. Arnold (submitted): Long-distance colonisation and radiation in gekkonid lizards, *Tarentola* (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences.
- Carranza, S., E.N. Arnold, R.H. Thomas, J.A. Mateo, & L.F. López-Jurado (1999): Status of the extinct giant lacertid lizard *Gallotia simonyi simonyi* (Reptilia: Lacertidae) assessed using mtDNA sequences from museum specimens. – *Herpetol. J.* 9: 83-86.
- Censky, E.J., K.Hodge & J. Dudley (1998): Over-water dispersal of lizards due to hurricanes. – *Nature* 395: 556.
- Coe, M.J., D. Bourn & I.R. Swingland (1979): The biomass, production and carrying capacity of giant tortoises on Aldabra. – *Phil. Trans. R. Soc. Lond. B* 286: 163-176.
- Greer, A.E. (1990): *The Biology and Evolution of Australian Lizards.* – Sydney: Surrey Beatty & Sons.
- Jaffe, M. (1994): *And no birds sing: the story of an ecological disaster in a tropical paradise.* – New York: Simon & Schuster.
- Joger, U. (1984): Die Radiation der Gattung *Tarentola* in Makronesien. – *Courier Forsch.-Inst. Senckenberg* 71: 91-111.
- Jones, C.G. (1993): The ecology and conservation of Mauritian skinks. – *Proc. Roy. Soc. Arts Sci. Mauritius* 5: 71-95.
- Kluge, A.G. (1969): The evolution and geographical origin of the New World

Hemidactylus mabouia-brooki complex (Gekkonidae, Sauria). – Misc. Pub. Mus. Zool. Michigan 138: 1-78.

Leguat, F. (1708): Voyages et Aventures de François Leguat & de ses Compagnons en deux îles désertes des Indes Orientales. – London: David Mortier.

Losos, J.B. , T.R. Jackman, A. Larson, K. de Queiroz, L. Rodríguez-Schettino (1998): Contingency and determinism in replicated adaptive radiations of island lizards. – Science 279: 2115-2118.

Loveridge, A. (1951): A new gecko of the genus *Gymnodactylus* from Serpent Island. – Proc. Biol. Soc. Wash. 64: 91-92.

MacArthur, R.H. & E.O. Wilson (1967): The theory of island biogeography. – Princeton: Princeton University Press.

Maddison, W.P. & D.R. Maddison (1996): MacClade 3.06. Sunderland, Massachusetts: Sinauer.

Mertens, R. (1963): The geckos of the genus *Phelsuma* on Mauritius and adjacent islands. – Maurit. Inst. Bull. 5: 299-305.

Mertens, R. (1966): Die nichtmadagassischen Arten und Unterarten der Geckonengattung *Phelsuma*. – Senck. Biol. 47: 85-110.

Mertens, R. (1970): Neues über einige Taxa der Geckonengattung *Phelsuma*. – Senck. Biol. 51: 1-13.

Pérez-Mellado, V., C. Corti & P. Lo Cascio (1997): Tail sutotomy and extinction in Mediterranean lizards. A preliminary study of continental and insular populations. – J. Zool. Lond. 243: 533-541.

Steadman, D.W. (1982): The origin of Darwin's Finches (Fringillidae, Passeriformes). – Trans. San Diego. Soc. nat. Hist. 19: 279-296.

Taylor, J.D. , C.J.R. Braithwaite, J.F. Peake & E.N. Arnold (1979): Terrestrial faunas and habitats of Aldabra during the late Pleistocene. – Phil. Trans. R. Soc. Lond. B 286: 47-66.

Townsend, C.H. (1936): Two giant tortoises were swept twenty miles by hurricane. – Bull. N. Y. zool. Soc. 39: 119-120.

Vaillant, L. (1899): Nouveaux documents historiques sur les tortues terrestres des Mascareignes et des Seychelles. – Bull. Mus. nat. Hist nat. Paris 5: 19-23.

Vinson, J. (1974): A new skink of the genus *Gongylomorphus* from the Macabé forest (Mauritius). – Rev. agric. suc. Ile Maurice 52: 39-40.

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Bird communities on the Comoro islands

Michel Louette

Abstract: Migrant birds include seabirds, Palaearctic waders, exceptional species (*Dromas ardeola* from Arabia and *Falco eleonora* from the Mediterranean) and occasional vagrants migrating from Africa to Madagascar. Waterbirds are remarkably scarce. Resident terrestrial birds are classified in relation to their presumed period of arrival: 9 (11?) "old" endemic species (non-Malagasy origin); 4 "new" endemic species (Malagasy origin) and 22 species represented by endemic subspecies; 17 non-endemic species, which probably arrived in recent times or still have gene flow. Ngazidja, highest, largest and most isolated island, is a centre of speciation. Smaller and lower Mwali is its satellite. Mayotte is another speciation centre. Ndzuani is poor in endemics. Using standardized point-transect counts, a general relationship between degree of endemism in the birds and preference for forest - presumably the original vegetation on much of the archipelago - was found, with some aberrations. The adaptation of endemics to degraded habitat is variable among species and among islands. This is also true for the adaptation of the non-endemic species to forest.

Key words: birds, Comoros, bird communities, endemism, habitat selection

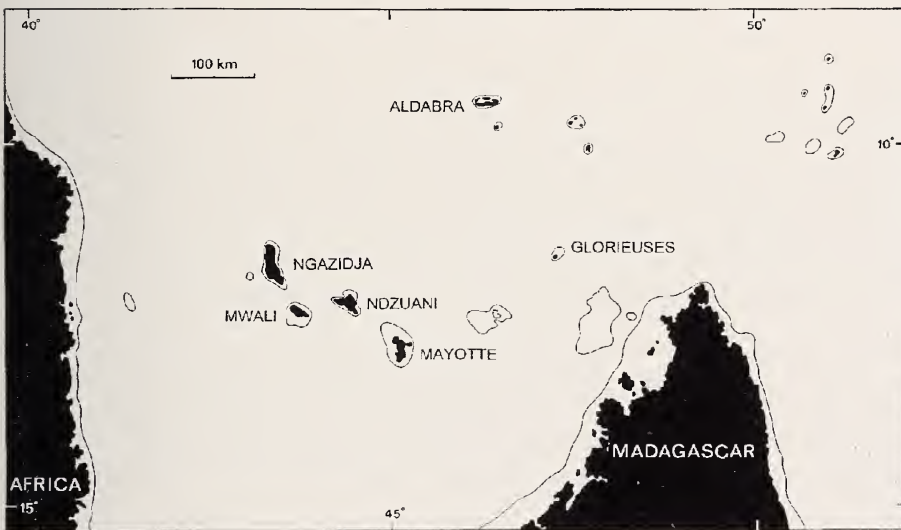


Fig. 1: Position of Comoro islands in the western Indian Ocean, with the 200 m line to show possible extent of land area after a sea level drop. Present-day land mass in black.

Study area

The Comoro archipelago lies midway between Madagascar and Africa (approximately 300 km distant from each - fig.1). The islands have never been linked with a continent and are isolated on all sides by seas more than 3000 m deep. Ngazidja is 1024 km² and rises to 2361 m at Mount Karthala; Mwali is 211 km² and rises to 790 m; Ndzuani is 424 km² and rises to 1595 m; Mayotte is 374 km² and rises to 660 m. The climate is humid and hot at sea level, but temperate at higher altitude on Ngazidja. Cyclones, though rarely devastating, occur frequently. The original vegetation is mostly evergreen forest, but above ca. 1500 m on Mount Karthala, the trees give way to stands of giant heath *Philippia comorensis* and, in drier parts of northern Ngazidja and southern and eastern Mayotte, to scrub (with such typical plants as Baobab trees *Adansonia digitata*), dating most probably from pre-human times. Mayotte has quite extensive stands of mangrove. The archipelago is of high biological importance (Stattersfield et al. 1998). Man settled about 1000 years ago and affected the environment and the avifauna. From sea level to ca. 600 m (much higher on Ndzuani), shifting cultivation and the development of villages resulted in a patchwork landscape of degraded forest, scrub and plantations of exotics (with many Coconut trees *Cocos nucifera*) and some badlands. Even at high altitude human influence is seen, due to cattle grazing and burning of the forest. The degradation is uneven: during the period of our visits, relatively intact forests were present on Ngazidja and Mwali (although not necessarily primary); in contrast, on densely populated Ndzuani only small remnants of forest persist, and on Mayotte a very limited area is under natural vegetation. But secondary forests occur on all peaks of Mayotte, dominated by introduced species with a prevalence of Mango trees *Mangifera indica* (and *Litsea glutinosa*) in the humid areas, and the deciduous *Albizzia lebeck* in the drier ones (Pascal 1997). Locally, isolated forest plantations of exotic trees occur. In the La Grille peak region of Ngazidja, there is a single stand of pure *Eucalyptus* sp.. In the centre of Mayotte, there are plantations of Teak *Tectona grandis* and West Indian Almond *Terminalia catappa* (amongst others) embedded in secondary forest in the northern lowest part of Bénara, and plantations of *Peltophorum pterocarpum* in the lowest part of Majimbini (Malagnoux 1991). Commercial forest exploitation occurs only on a small scale. Crops are much in evidence. Typical for the Comoros are trees such as Ylang-ylang *Cananga odorata* and Clove *Syzygium aromaticum* (the latter especially on Ndzuani and Mwali); Vanilla *Vanillia fragrans* is still present, but Sugarcane *Saccharum officinarum* monoculture was abandoned a century ago. Vines and other weeds abound, with *Lantana camara* dominating in the drier parts.

Methods

For the taxonomic study, a large number of specimens was examined in major natural history museums in at Tervuren, London, Paris, Leiden and New York. Taxa were considered as species or subspecies based on morphology (Louette 1988).

Birds were observed by a team during near-annual visits of several weeks per year in 1983-1998. Furthermore, essentially in order to compare bird diversity and the habitat choice of the endemic (forest) species, standardized point-transects were

counted (according to the method described by Hustings et al. 1985) by two observers, on Ngazidja at 33 stations, during the years 1985 and 1989; on Mayotte at 9 stations during each of three consecutive years 1992-1994; on Mwali at 3 stations in 1985 and at 2 stations by one observer in 1989 (complete descriptions in Louette et al. 1988b, Stevens et al. 1995, Stevens & Louette 1999); incomplete counts at 6 stations on Ndzuani in 1992 by the author alone are also available. Here, these data are reanalysed in order to compare communities on the different habitats on the islands and to discuss the adaptation of bird species to available habitat. Simply considering an altitudinal gradient would not be appropriate, because the amount of degradation differs among the islands and Ngazidja is unique in having a montane zone above the tree line. Habitat types for the present analysis are listed in the legend of figs.2-9. Number of birds seen per unit time and per habitat type (a sum of stations) is used as a parameter in the ecological profile. Nocturnal birds and migratory water birds are not considered.

Status and origin of the birds

Faunistics, taxonomy, origin and evolution were studied by Benson (1960) and by Louette (1988, 1992, 1996), which are the main sources for the following discussion.

a. Migrants

This archipelago is at the crossroads of several bird migration routes, although there are almost no passerines, except rarely Hirundinidae:

– Waders from Palaearctic breeding grounds, wintering on the coasts of the southern oceans in general; the most common ones in the Comoros are: *Arenaria interpres*, *Pluvialis squatarola*, *Charadrius leschenaultii*, *C. hiaticula*, *Numenius phaeopus*, *Actitis hypoleucos*, *Tringa nebularia*, *Calidris ferruginea*. It is doubtful however if any one of them ever attains numbers of "Ramsar Convention" importance (1% of world population).

– The enigmatic *Dromas ardeola* from the Horn of Africa and Arabia (significant because it is a localized species: Hockey & Aspinall 1996). This is an important wintering area: several tens of individuals can be found together at favourite sites.

– The specialized *Falco eleonora* from the Mediterranean (important because a localized species). Several individuals (up to 4) were observed together at particular sites.

– An array of species represented by a small number of individuals: *Ardeola idae*, rarely *Phoenicopiterus ruber*, *Glareola ocularis*, *Eurystomus glaucurus*, and *Coturnix delegorguei* which was only recently discovered! All these are on the passage from Madagascar to Africa. No migrants from Asia to Africa have been recorded so far.

– Terns *Sterna* spp. in hundreds, especially *S. bengalensis* and *S. bergii*, also *Anous stolidus* (plus a few *Fregata* spp. and *Sula* spp.), from the Indian Ocean region.

– Shearwaters Procellariidae spp. and Storm Petrels Hydrobatidae spp. from the Indian Ocean (and possibly even the Pacific Ocean).

b. Breeding waterbirds

Very few breeding pairs are present:

– *Phaethon lepturus* at favourite localized spots on the coast of the four islands;

- Shearwaters *Puffinus lherminieri* and Gannets *Sula dactylatra*, only on Mwali;
- Grebes *Tachybaptus ruficollis* on all the freshwater lakes of which each island has one;
- Herons *Bubulcus ibis*, *Ardea cinerea*, *Egretta alba* (very few pairs).

c. Breeding land birds

The Comoro land avifauna is a rather impoverished mixture of Madagascan and African elements with a high proportion of endemic species and subspecies. Endemism is favoured by geography (separate islands, pronounced relief and sufficient size), the originally rich habitats of the islands and (especially) the distances between the islands and also from other regions restricting gene flow. It is debatable if the Comoro avifauna is impoverished or on the contrary fairly complete. None of the surrounding areas are really comparable, because Madagascar is very large and was separated a long time ago from other continents, the Mascarenes are truly oceanic, Pemba is much closer to Africa and colonized to a very large extent (but not completely!) from there. Other archipelagos in the area consist of much smaller or flat islands (such as the granitic Seychelles or the atolls of the Aldabra group) but their bird communities are similar to that of the Comoros, although more impoverished.

Affinities and estimated age of arrival are diverse. Three groups, related to their apparent period of arrival, can be recognized (for a complete list see Louette 1988):

- A first wave: 9 ancient endemic species of non-Malagasy, probably African, origin present on one or more islands. The recently described *Otus moheliensis* from Mwali (Lafontaine & Moulaert 1998) and *O. capnodes* from Ndzuani seem to be good species and different from *O. pauliani* from Ngazidja, bringing the total number of species in this group to 10 or even 11.
- A second wave: 4 modern endemic species and 22 species represented by endemic subspecies, probably separated from the source population in Madagascar more recently.
- Non-endemic species that arrived presumably in modern times, or which have regular gene flow with their source area. They are indistinguishable from forms in Madagascar (5), Africa (4) or both areas (8). Some of them arrived unaided by man, but their establishment was made possible by his activities, while others were deliberately introduced.

How can the composition of the first and second waves be explained? Louette (1996) gave the following reasoning. The Comoros are roughly equidistant from the present-day African and Madagascar coasts. However, the prevailing winds nowadays are from the direction of Madagascar for much of the year, which would favour colonizers from that direction (although winds may have been different in the distant past). Colonization from Madagascar may have been particularly favoured at certain periods by the presence of 'stepping-stones' towards the Comoro archipelago. During episodes of glaciation in the Pleistocene, the sea level was apparently several tens of metres lower than at present. As a result the north-western Madagascar coast would have been greatly extended, as would the Glorieuses, and two supplementary islands would have existed east of the Comoros (see model, based on 200 m sea level lowering, in fig. 1). The distance to the African coast, however, would have been very little changed from what is today. These factors may have decreased the chance of a

definitive isolation of colonists from Madagascar compared to those from Africa, so that endemic species originating from Madagascar would appear to be younger. A general rise in sea level would have had little effect on the size of the four Comoros, although perhaps most on Mayotte.

The peculiarities of the four islands are as follows: Ngazidja, highest, largest and most distant in the archipelago, is a centre of speciation; smaller and lower, Mwali is its satellite. Mayotte is another, smaller speciation centre (somewhat surprisingly, considering its proximity to Madagascar). The central island, Ndzuani, is poor in endemics; it shows affinities with Aldabra, sharing a few species of direct Madagascan origin not found elsewhere on the archipelago.

Was island-hopping or independent colonization from the mainland prevalent in this archipelago? Multiple colonizations from one source have been demonstrated in several genera (Louette & Herremans 1985, Louette et al. 1988a). These were separated by large time intervals, resulting in a different faunal composition on each island. Nevertheless, the checkerboard pattern of forms in *Nectarinia* on the islands proves that colonizations of birds belonging to one genus may have arrived from different directions.

The hypothesized histories of birds are based on their characteristics on each island, their interrelationship and the relationship with neighbouring areas; unfortunately this exercise deals only with surviving species because no important fossils are yet known.

Adaptation to the environment

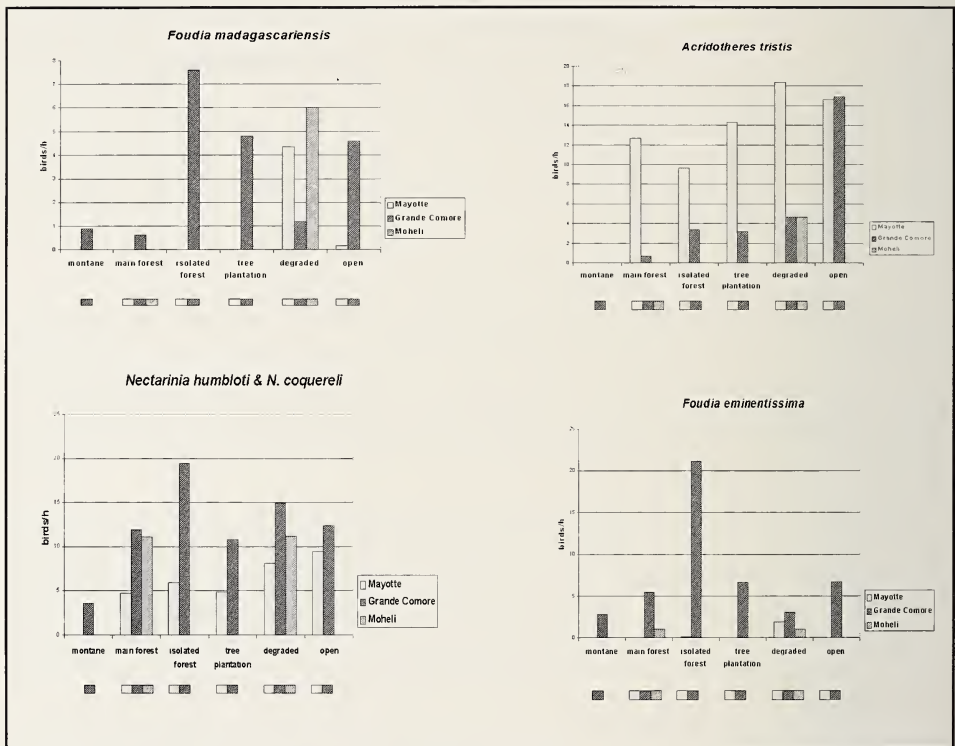
It is possible that substantial parts of the avifauna have disappeared since the arrival of man. Strict forest specialists come to mind as possible extinctions. It is likely that only those species successful in adapting to a new situation survive on such small islands. Indeed, some endemics now live outside forest habitats on some or on all islands. The capacity of the original birds to survive in the new anthropogenic habitats is analyzed below.

A general correlation of degree of endemism in bird taxa with preference for forest (presumably the original vegetation on much of the archipelago) was demonstrated on Ngazidja (Stevens et al. 1995), on Mwali (Louette et al. 1989) and on Mayotte (Stevens & Louette 1999). The present paper also documents habitat selection by recent arrivals, after man-altered habitats became available. This analysis is mainly based on the comparison of the two most extreme and best explored islands: Ngazidja and Mayotte.

Ngazidja (= Grande Comoro)

This is the largest island, and alone of the islands has large areas of high altitude terrain. It also has most primary forest and the highest level of endemism (Louette 1988). Generally speaking, endemism increases with altitude, so that above 1000 m nearly all birds belong to endemic species or subspecies. In the main forest on Mount Karthala, endemic species reach their highest densities in the undisturbed areas (Stevens et al. 1995) and diversity of endemism is highest in the wettest area (Stevens et al. 1993). A major shift occurs at medium altitude, where there is an edge effect. The density of endemic species increases up to about 1000 m and remains numerous to 1700 m, after which it decreases. Endemic subspecies are found from sea level to

the highest peaks with largest numbers at 400–1500 m. Non-endemic species are most numerous below 800 m and uncommon at higher altitudes. In the isolated forest of La Grille (on the smaller volcanic peak of Ngazidja) and in pure *Eucalyptus* plantation, at 700–900 m, a large proportion of non-endemics compensates for the absence of endemic species. It is well known that species richness decreases with altitude (Brown & Gibson 1983) due to less diverse vegetation and a smaller available surface at higher altitudes. Such a model predicts more species at lower altitudes. Since the data on Ngazidja do not fit this general model it can be supposed that a number of stenotopic endemic species from lower altitudes are extinct, or that the endemic species now found at mid-altitudes preferred originally low-altitude forest (Louette & Stevens 1992). Presumably, as a result of human activities at lower altitudes on Mount Karthala and the consequent disappearance of the lowland forests, some



Figs.2-5: Mean number of individual birds counted per hour in 6 habitat types for 4 selected species

- On Ngazidja (= Grande Comore) six habitat types: montane (J) - main forest (A-F) - isolated forest (G) - tree plantations (H) - degraded mosaic (K-L) - open terrain (I) (letters in brackets stand for the restricted habitat types in Stevens et al. 1995)

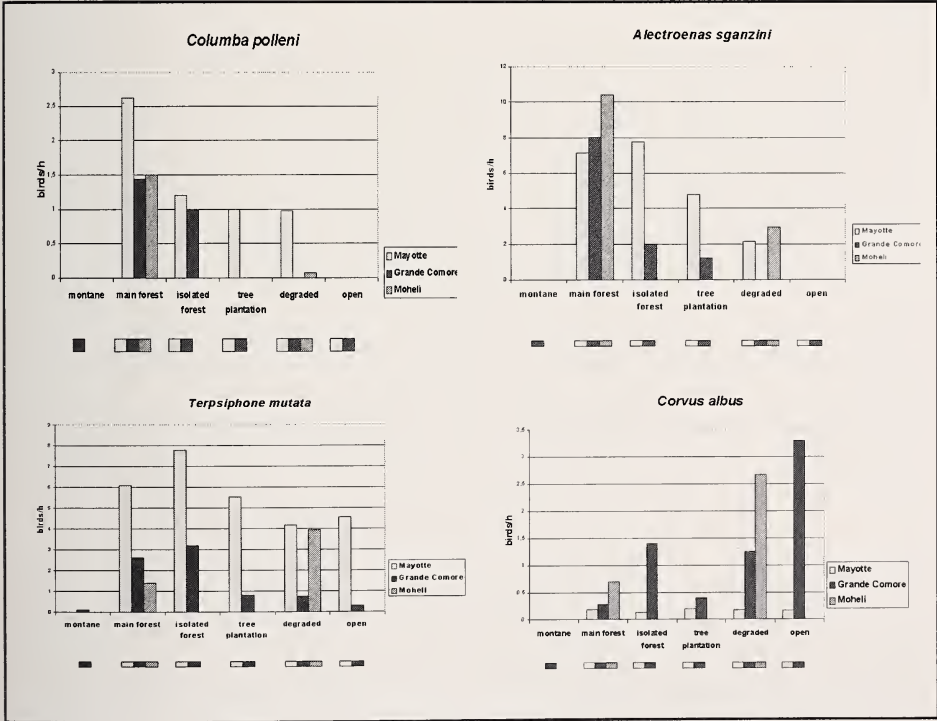
- On Mayotte five habitat types: main forest (all stations except the following) - isolated forest (Choungui) - tree plantation (Bénara low and Majimbini low) - degraded mosaic (Combani and Ochoungui low) - open terrain, including mangrove (Mireremi and Dzoumogné) (see Stevens & Louette 1999)

- On Mwali, along the transect from Miringoni towards Chalet St Antoine two habitat types: forest (upper) - degraded mosaic (middle and lower altitudes) (see Louette et al. 1989)

endemic species unable to move upwards became extinct or nearly so, such as *Dicrurus fuscipennis*, which is very localized in lowland forest. The fact that the non-endemics – the latest arrivals on the island – are also restricted in range could be due primarily to altitude, and – despite the supposed disappearance of some endemics – to unsuitable vegetation structure. At 700–900 m on La Grille non-endemics such as *Foudia madagascariensis* (fig.2) and *Acridotheres tristis* (fig.3) readily enter isolated forest remnants and the *Eucalyptus* plantation.

Mayotte

Mayotte is the least elevated island and consequently all forests are situated lower than the lowest forests on Ngazidja. The forests are secondary and the rainfall gradient is moderate. Endemic species are more common in the forest, except *Nectarinia coquerelii* (fig.4). Forest is still utilized, but to a lesser extent, by several endemic subspecies, others utilize different habitats, such as *Foudia eminentissima* (fig.5), a forest bird elsewhere in the archipelago and on Madagascar (Adriaensen et al., in press). Strikingly, the abundant predator *Accipiter francesii* shows no preference for forest. All non-endemic species are more common in non-forest habitats, but to varying degrees. Thus, *Acridotheres tristis* (fig.3) readily enters forest here. Often this process is called habitat choice, but in fact on such small islands



Figs.6–9: Mean number of individual birds counted per hour in 6 habitat types for 4 selected species; sites and habitat types as in figs.2–5.

there is simply no choice, and tolerance of the existing habitat is a precondition of survival.

What do we know about the situation on the two other islands?

On Mwali, endemic diversity is high and several endemic birds adapt better to secondary vegetation than on Ngazidja. On Ndzuani, few forests remain, but some endemics survive, showing even stronger capacity for adaptation to changed conditions, the most remarkable case being that of *Alectroenas sganzini*.

Species groups

Old endemic species

A few of these are narrowly restricted to high altitude and forest. Others show adaptation: *Columba polleni* (fig.6) prefers forest (main block rather than isolated remnants) everywhere, but on Mayotte it accepts secondary forest and tree plantations. *Turdus bewsheri* adapts rather well to degraded habitat. *Nectarinia* spp. are best adapted, probably because flowers, their food source, became more abundant and diverse after man's arrival. On Mayotte, the *Dicrurus* species, although not omnipresent, adapted to non-forest, while the equivalent species on Ngazidja was unable to do so.

New Endemic species

Alectroenas sganzini (fig.7) evolved on the Comoros from *A. madagascariensis* parent stock, a stenotypic forest bird. It prefers forest when this habitat is available and on Ngazidja it lives in logged forest (Stevens et al. 1995). It occurs rarely in non-forest habitats on Mayotte and Mwali, the islands where forest is scarce nowadays, but on Ndzuani it was readily observed in degraded habitat, even at sea level. It has adapted to non-forest on Aldabra which it colonized from the Comoros, evidently because no real evergreen forest is present on this atoll. Other new endemics are restricted to forest. On Ngazidja and Mwali, the first arrival, now a separate species, *Hypsipetes parvirostris* excludes the second arrival *H. madagascariensis* from the forest at higher altitude (Louette & Herremans 1985). In *Nesillas*, two separate invasions led to sympatry on Mwali (*N. mariae* and the endemic race of the Madagascan *N. typica*, which occupy different niches). *N. brevicaudata* – possibly the precursor of *N. mariae* of Mwali – lives at medium and high altitude on Ngazidja. *N. typica longicaudata*, presumably an independent and more recent colonist, is widespread on Ndzuani. It is surprising that some *Nesillas* taxa are restricted to higher zones while others occupy the whole island (Louette et al. 1988a).

Endemic subspecies

Accipiter francesii lives on Mayotte at very high breeding densities in degraded forest; in the non-breeding season it occurs in the drier parts of the island. On Ngazidja it is restricted to, and rather uncommon in, the well forested zone, but on Ndzuani it is generally uncommon and it is absent on Mwali. *Streptopelia picturata* is most numerous in forest, but it does occur in numbers outside; the trend is reversed on Mwali. From its morphology, the race of *Terpsiphone mutata* (fig.8) on Mayotte is a recent arrival and is ubiquitous. The older races on the other islands are scarcer, the one on Ngazidja preferring forest. On Mwali the density trend is reversed.

Zosterops maderaspatanus is more numerous outside forest on Ngazidja. *Foudia eminentissima* (fig.5) is widespread on Ngazidja, where it apparently has a specific niche (Louette 1988) while on Mayotte it is curiously restricted to open places (Adriaensen et al., in press).

Non-endemic species

Circus maillardi is well adapted to forest and, surprisingly, does not occupy open terrain. It occurs on the three western islands, but is absent on Mayotte. *Milvus migrans*, a commensal raptor in Africa, should seemingly benefit from the man-altered habitat where it used to occur, but recently became extinct (Louette 1993). *Numida meleagris* is probably restricted by hunting and *Agapornis cana* possibly by trapping. *Streptopelia capicola* occurs commonly only in dry habitat, as in Africa, but *Turtur tympanistria* avoids high altitudes and evergreen forest and is rare in the Comoros, although there is no apparent competitor. This is a forest species in Africa, living in high rainfall areas and going readily up to 2500 m in Kenya (Zimmerman et al. 1996). *Corvus albus* (fig.9) is rather uncommon on the four islands, where it has been present since immemorial times, so it is difficult to understand why it should be so rare on Mayotte. Likewise, *Lonchura cucullata* is a self-introduced species, restricted to grasslands and localized to gardens. It may be asked why *Foudia madagascariensis* (fig.2) is not more common. On Réunion, Barré (1983) notes it represents 35% of the bird population in "savane boisée" and is less common but present in all habitats. On that island it is replaced by *Passer domesticus* in urban environments, which it occupies in the Seychelles where the latter species is lacking. In Mauritius, *F. madagascariensis* is common, nesting even at greater altitude but at lower densities than in the lowlands and is not really a competitor of the endemic Fody (*Foudia eminentissima*) (Cheke 1987). *Passer domesticus* is almost limited to coastal areas with western-style buildings. It used to be widespread in Mwali and became extinct in Ndzuani, which is the most degraded island! This is a surprisingly 'poor performance' for such an opportunistic generalist species that has conquered all continents and many islands. *Acridotheres tristis* (fig.3), introduced in the Comoros at the beginning of the century, is the most successful non-endemic species. Nowadays it is the commonest bird, alongside species of *Hypsipetes*, *Nectarinia* and *Zosterops*. It seems also the only one that has occupied a new niche (forest).

It is clear that the recently arrived species have only adapted to a variable and limited degree to the Comoro habitats.

Conservation

Tropical forests on islands are among the most threatened habitats in the world (Vickery 1998). The Comoros are still relatively intact, but deforestation and introduction of exotics have taken their toll. The impact of rats is very important and, when these are present, longevity becomes a more important factor than breeding success for birds. Relative numbers of specialist forest species are often reduced in disturbed forest (Bennun & Fanshawe 1997) but this is not very apparent in the Comores. It is the case though on Ndzuani, the most disturbed island, which nevertheless still has some endemics (although the populations may not be viable over long periods). Mwali is the most intact island: there are low numbers of

Acridotheres tristis or *Foudia madagascariensis* in the forest and all endemics are in the “correct” forest to degraded forest habitat, except the well adapted *Terpsiphone mutata* (and also *Foudia eminentissima*, which is unaccountably scarce). The lowlands of Ngazidja are badly degraded, but the forest at higher altitudes on Mount Karthala was relatively intact at the time of our study; the isolated forest on La Grille, however, is doomed. Mayotte is surprising: the forest has been settled by *Acridotheres tristis*, but why are other invasive species such as *Foudia madagascariensis* and *Corvus albus* so scarce? The isolated forest is less acceptable to *Columba polleni* and avoided by *Dicrurus waldenii*. In general it is clear that tree plantations are a very poor replacement habitat for forest, but the spontaneous “Mango” forests of Mayotte at least retain some endemic elements and enable the survival of part of the original avifauna, already adapted to a less luxuriant environment. Rapid destruction of rain forests on the islands of Mwali and Ngazidja would probably eliminate the less flexible endemic bird taxa.

As to the migrants, the “overwintering” *Dromas ardeola* population deserves to be monitored; specific research is needed on its ecology and its mortality should be monitored.

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References

- Adriaensen, F., M. Louette, J. Stevens, W. Plompen & G. Verheyen (2000, in press): Distribution of the Forest Fody *Foudia eminentissima algondae* on the island of Mayotte. – Ostrich.
- Barré, N. (1983): Distribution et abondance des oiseaux terrestres de l’île de la Réunion (Océan Indien). – Rev. Ecol. (Terre Vie) 37: 37-85.
- Bennun, L., & J. Fanshawe (1997): Using forest birds to evaluate forest management: an East African perspective. – www.uk.earthwatch.org/africa.
- Benson, C.W. (1960): The birds of the Comoro islands: results of the British Ornithologists’ Union Centenary expedition. – Ibis 103b: 5-106.
- Brown, J.H., & A.C. Gibson (1983): Biogeography. – C.V. Mosby, Saint Louis.
- Cheke, A.S. (1987): The ecology of the smaller land birds of Mauritius. – pp 151-207 in: Studies of Mascarene land birds. (ed. Diamond, A.W.). – Cambridge University Press, Cambridge.
- Hockey, Ph., & S.J. Aspinall (1996): The Crab Plover, enigmatic wader of the desert coasts. – Africa Birds & Birding 1: 60-67.
- Hustings, M.F.H., R.G.M. Kwak, P.G.M. Opdam & M.J.S.M. Reynen (1985): Vogelinventarisatie. Achtergronden, richtlijnen en verslaggeving. – PUDOC, Wageningen, Netherlands.

- Lafontaine, R.-M., & N. Moulaert (1998): Une nouvelle espèce de petit-duc (*Otus*, Aves) aux Comores: taxonomie et statut de conservation. – J. Afr. Zool. 112: 163-169.
- Louette, M. (1988): Les Oiseaux des Comores. – Ann. Mus. r. afr. Centrale (Zool.) 255: 1-192.
- Louette, M. (1992): The origin and evolution of Comoro land birds. – Proc. VII Pan-Afr. Orn. Congr. (Nairobi): 207-215.
- Louette, M. (1993): Decrease of the Black Kite *Milvus migrans* and other commensal birds in the Comoros. – Scopus 17: 14-18.
- Louette, M. (1996): Biogéographie, origine et évolution des oiseaux aux Comores. – pp. 337-348 in: Biogéographie de Madagascar. (ed. Lourenço, W.R.). – ORSTOM, Paris.
- Louette, M., & M. Herremans (1985): Taxonomy and evolution in the bulbuls (*Hypsipetes*) on the Comoro Islands. – Proc. Intern. Symp. African Vertebr., Bonn: 407-423.
- Louette, M., M. Herremans, L. Bijnens & L. Janssens (1988a): Taxonomy and evolution in the brush warblers *Nesillas* on the Comoro Islands. – Tauraco 1: 110-129.
- Louette, M., J. Stevens, L. Bijnens & L. Janssens (1988b): A survey of the endemic avifauna of the Comoro Islands. Study Report, 25. – ICBP, Cambridge.
- Louette, M., L. Bijnens, J. Stevens & L. Janssens (1989): Comparison of forest bird communities on Ngazidja and Mwali (Comoro Islands). – Ostrich Suppl. 14: 33-37.
- Louette, M., & J. Stevens (1992): Conserving the endemic birds on the Comoro islands. I: general considerations on chances for survival. – Bird Conserv. Int. 2: 61-80.
- Malagnoux, M. (1991): Mission d'appui au secteur forestier. – Report to Service des Eaux et Forêts, Mayotte.
- Pascal, O. (1997): La végétation naturelle à Mayotte. – Direction de l'Agriculture et de la Forêt (Mayotte).
- Stattersfield, A.J., M.J. Crosby, A.J. Long & D.C. Wege (1998): Endemic bird areas of the world. Birdlife Conservation series N°7. – Birdlife, Cambridge.
- Stevens, J., M. Louette, L. Bijnens & M. Herremans (1993): Bird diversity on Ngazidja, Comoro Islands. – Proc. VIII Pan-Afr. Orn. Congr. (Bujumbura): 179-186.
- Stevens, J., M. Louette, L. Bijnens & M. Herremans (1995): Conserving the endemic birds on the Comoro Islands, III: bird diversity and habitat selection on Ngazidja. – Bird Conserv. Int. 5: 463-480.
- Stevens, J., & M. Louette (1999): Land bird abundance and the conservation of endemism on the island of Mayotte (Indian Ocean). – Alauda 67: 123-139.
- Vickery, J. (1998): Report on the BOU's Tropical Forests and Islands Conference. – www.bou.org.uk/meetrep.

Zimmerman, D.A., D.A. Turner & D.J. Pearson (1996): Birds of Kenya and northern Tanzania. – C. Helm, London.

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The reptile fauna of the Soqotra archipelago

Ulrich Joger

Abstract: During a four-week faunal survey of Soqotra and its smaller satellites Semha and Abd El Kuri, as part of the UNDP/GEF project 'Conservation and Sustainable Use of the Biodiversity of Soqotra Archipelago', most of the resident reptile species were collected, including at least 4 undescribed taxa.

The vertebrate fauna of Soqotra is dominated by lizards, especially geckos, this family making up two-thirds of the approximately 30 reptile species, 27 of them being endemic. On Semha and Abd El Kuri, local endemic gecko species occur. Three lizard genera and one snake genus are endemic to the archipelago. The predominant biogeographic affiliation of the Soqotran reptile fauna is Afrotropical.

Key words: Soqotra archipelago, herpetofauna, endemism

Introduction

The Soqotran archipelago in the northwestern Indian Ocean, politically part of the Republic of Yemen, consists of three inhabited and a number of uninhabited islands. Geologically, they comprise the peaks of a submarine ridge in continuation of the northern Somalian highlands. However sea depth between Cap Guardafui on the Horn of Africa and Abd El Kuri, the nearest island of the archipelago about 90 km to the east, is between 200 and 1000 m, thus beyond Pleistocene sea level changes. If the separation of these islands was associated with the tectonic processes that lead to the formation of the Gulf of Aden and the Red Sea, it could be dated, with some reservation, to the first half of the Tertiary (older than 30 million years b.p.; see Girdler 1984). Therefore there should have been both a basic continental (African) faunal stock as well as plenty of time for the considerable evolution of a specific island fauna.

The individual islands are geologically similar (mainly limestone plateaus with coastal strips of limited extension) but different in size, climate and vegetation.

Soqotra, the major island, has an area of approximately 3600 km² (3625 km² according to Wranik 1998a), mountain peaks (the central Haghier range reaches 1500 m and frequent fogs are present), abundant water and a rich savannah-like vegetation dominated by trees or shrubs of the genera *Croton*, *Boswellia*, *Adenium*, *Dendrosicyos*, *Euphorbia* and *Dracaena* (fig.1). The total flora of the archipelago amounts to at least 850 species, of which many are endemic (Miller & Bazara'a 1998). Abd El Kuri (162 km²) and Semha (45 km²) also reach heights of up to 800 m, but are considerably drier, with no permanent streams and a succulent flora largely devoid of trees except a few *Euphorbia* (fig.2). Traditional agriculture is based on livestock (Soqotra and Semha) and date plantations (mainly Soqotra).



Fig.1: Slope with *Dracaena* trees to the north of Kilisan, central eastern Soqatra. Habitat of *Haemodracon riebecki* and *Hemidactylus* sp. (description in preparation).

Until recently, the faunal exploration of the archipelago has scratched only the surface of the total fauna. After a number of expeditions at the end of the 19th and the beginning of the 20th centuries (Günther 1881, Peters 1882, Dixey et al. 1898, Forbes 1903, Steindachner 1903), the islands were ignored by zoological researchers. This was mainly due to geographical as well as political isolation. Only limited field work was possible during the time of southern Yemeni independence (Wranik et al. 1986). An overview of animal taxa known from Soqatra prior to our expedition was given by Wranik (1998a).

This report is based on a four-week stay on Soqatra, Semha and Abd El Kuri during the whole of February 1999, as participants of the UNDP/GEF project 'Conservation and Sustainable Use of the Biodiversity of Soqatra Archipelago', which aimed at compiling an inventory of fauna and flora of the archipelago in order to design a master plan for conservation (Joger et al. 1999).



Fig.2: *Euphorbia* tree in the interior of Semha.

Results and Discussion

Endemism and biogeographic relations

The vertebrate fauna of the Soqotran archipelago is dominated by reptiles and birds. All freshwater fishes found so far belong to introduced species or represent secondary invaders from the marine environment. Amphibians do not exist. This paucity of freshwater vertebrates may be attributed to a combination of varying aridity in the geological past and the ubiquitous presence of voracious freshwater crabs (Potamidae). Most wild mammal species have been introduced, such as mice (*Mus musculus*), rats (*Rattus rattus*), and civet cats (*Viverricula malaccensis*). However, the speculation of Wranik (1998a) that the Soqotran fauna originated "before mammals appeared on earth" must be strongly rejected. This would imply a separation in Triassic times (approximately 200 million years b.p.) – which is not in accordance with tectonic evidence. Possible candidates for endemic mammal taxa are bats (*Rhinopoma* sp.) and a shrew (*Suncus* sp.) which we found on Soqotra. The specimens are under study.

The avifauna of the Soqotra archipelago is comparatively well known and comprises 31 breeding species, of which 6 species and 10 or 11 subspecies are considered endemic (Al Sagheir & Porter 1998). This rather low number of endemics could have been expected in animals capable of flying, and is found to be similar in dragonflies (Schneider & Dumont 1998). In contrast, among approximately 30 reptile species present, only 3 geckos of the genus *Hemidactylus*

Soqotran Reptile Genera

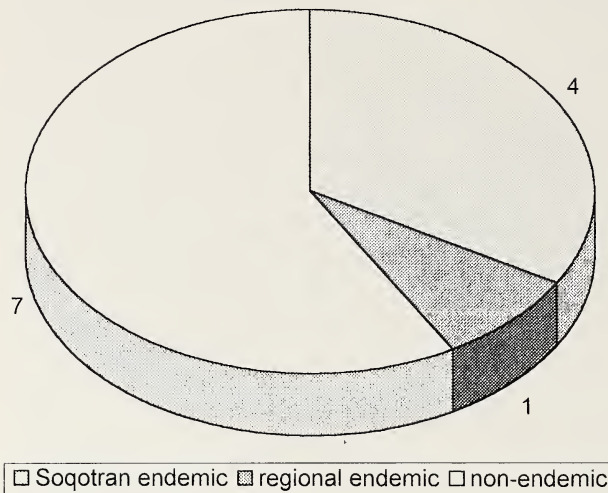


Fig.3: Genus level endemism in Soqotran reptiles.

(10%) also occur outside Soqotra and are likely to have been introduced by man. At least two of them (*Hemidactylus turcicus* and *H. flaviviridis*) frequently occur in and around human habitations. Thus the indigenous reptile fauna can be considered 100% endemic. Even one third of genera are endemic (fig.3), namely the gekkonid *Haemodracon* Bauer, Good & Branch, 1997, the scincid *Parachalcides* Boulenger, 1899, the trogonophid amphisbaenian *Pachycalamus* Günther, 1881 (fig.4), and the colubrid *Dityophis* Günther, 1881 (fig.5). A regional or subendemic genus is the diurnal gekkonid *Pristurus*, which occurs in the countries bordering the Red Sea and the Gulf of Aden. Its sister genus appears to be *Quedenfeldtia* from southwestern Morocco, a relict area where a pre-Saharan fauna, including *Trogonophis*, a relative of *Pachycalamus*, occurs¹. *Haemodracon* may be part of



Fig.4: *Pachycalamus brevis*, the endemic Soqotran amphisbaenid.

¹ The remaining genera of the Trogonophidae are *Diplometopon* from eastern Arabia and *Agamodon* from Yemen and Somalia.



Fig.5: *Dityophis vivax*, one of the two endemic Soqotran colubrids.

an Afro-Malgasian group of leaf-toed geckos (Bauer et al. 1997). *Dityophis* was considered related to the Afro-Malgasian genera *Pythonodipsas*, *Geodipsas* or *Dipsadoboa* (= *Thamnodynastes*) (Günther 1881, Bogert 1940, Parker 1949). *Parachalcides* resembles the South African genus *Sepsina* (Boulenger 1903). Although the real evolutionary relationships of these genera will be analyzed using molecular techniques, it can be stated that the fauna is of predominantly Afro-Malgasian or Afro-Arabian (pre-Saharan) origin, and the disjunct distribution of groups and the high diversification point to an ancient separation of these taxa (Joger 1987).

Among endemic species of non-endemic genera, the Soqotran chameleon (*Chamaeleo monachus* Gray, 1864) clearly belongs to the mainland African/west Asian genus and subgenus *Chamaeleo* s.str., not to the Malgasian radiation (Klaver & Böhme 1986). Its type locality "Madagascar" must therefore be erroneous, and Wranik's (1998a) consideration that it might have been imported by man is also contradicted by the fact that it does not occur elsewhere.

The endemic nocturnal geckos of the genus *Hemidactylus* are rather diverse, but most of them resemble one or the other Somalian species. Somalia can be considered an area of primary radiation of the genus (Joger 1985). It should be noted that Abd El Kuri, the island closest to Somalia, harbours two *Hemidactylus* species of its own (*H. forbesii* Boulenger, 1899 and *H. oxyrhinus* Boulenger, 1899).

The scincid *Mabuya socotrana* (Peters, 1881) also appears related to African congeners. The lacertid lizard *Mesalina balfouri* (Blanford, 1881) is similar to *M. guttulata*, a Saharo-Sindian species (Boulenger 1903). The colubrid snake *Coluber socotrae* (Günther, 1881) is probably allied to the Afro-Arabian *C. florulentus* group (Parker 1949).

Little can be said about the affiliations of the three blind snakes of Soqotra: *Leptotyphlops filiformis* (Boulenger, 1899), *L. macrura* (Boulenger, 1899), and *Typhlops socotranus* Boulenger, 1889. The former is similar to the Saharo-Arabian *L. macrorhynchus*, the latter has been considered a relative of *T. cuneirostris* from Somalia (Parker 1949).

Missing families and genera; erroneous records

Land tortoises were mentioned in a Greek report from the 1st century A.D. on “Dioscurida” - an island later identified as Soqotra (Schoff 1912, from Schneider 1996). Today only sea turtles nest on the archipelago. Taking into account that large tortoises used to live on many Indian Ocean islands such as the Seychelles, Aldabra, Madagascar and the Mascarenes, where they were eradicated by sailors, settlers and introduced predators (Arnold 1981), there is some likelihood for this (although no tortoise bones or shells have been found so far on Soqotra).

As the same report also mentions large lizards, Wranik (1998a, b) speculates about the occurrence of a now extinct *Varanus*. However this is unlikely. Contrary to land tortoises, varanids have never been reported from other western Indian Ocean islands. Instead, large scincids and gekkonids are known from some of them (Arnold 2000, this volume). The explanation for their absence is that varanids originated in southeast Asia or Australia (where they still have their greatest diversity) and invaded Africa and Arabia only during the Miocene (18-20 million years b.p.), when the Tethys' Sea had been interrupted by tectonic upheavals associated with the collision of the Afro-Arabian plate with continental Asia. The few *Varanus* species living in Africa and Arabia today have been found to be closely related to each other (Böhme et al. 1989) and can therefore be regarded as descendants of a rather recent invader – after Soqotra had been separated from the African continent.

A similar biogeographical history can be assumed for the Agamidae – a family present everywhere in Australia, Asia and Africa, except on Madagascar and the islands of the western Indian Ocean. On Madagascar their ecological niches are occupied by the otherwise New World iguanids. A fossil iguanid has been reported from Aldabra (Arnold 1981). Joger (1986, 1991) reconstructed the phylogeny of the two agamid subfamilies, Agaminae and Uromastycinae, and found that in both, Arabian and African radiations are much more recent than Oriental ones. They also reached East Africa after the separation of Soqotra. A record of *Uromastyx ocellatus* from Soqotra (Peters 1882) can be regarded as a locality error, since a chameleon from mainland Yemen (*Chamaeleo calyptratus*) was recorded from Soqotra in the same article.

Among the Gekkonidae, two names have been deleted from the faunal list of Soqotra. *Ptyodactylus sokotranus* Steindachner, 1902, described from Soqotra, was later found to be a synonym of *Phyllodactylus* (= *Haemodracon*) *riebecki* (Eiselt 1962), a fact that was overlooked by Wermuth (1965). The Soqotran population of *Pristurus rupestris*, a mainland gecko recorded from Soqotra by Peters (1882) and Boulenger (1903), was later described as *P. sokotranus* Parker, 1938.

The saw-scaled viper *Echis coloratus* was recorded from Soqotra by Balfour (Günther 1881) and controversially discussed by Parker (1949), Corkill & Cochrane (1965), Joger (1984) and Wranik (1998a, under the wrong name *Echinus coloratus*). During our survey, large black snakes resembling a cobra (*Naja* sp.) were observed at higher altitudes on Soqotra and Semha, but not caught. Although *Echis* and *Naja* are of African origin (Joger 1987) and thus possible original inhabitants of Soqotra, there are no records of venomous snakes or fatal snake bites among the human population.

Echis coloratus, like *Chamaeleo calytratus* and *Uromastix ocellatus*, occurs in Yemen and its Soqotran record can be attributed to a locality error, while the black snakes are most likely old melanistic individuals of *Coluber socotrae*.

Comparison between individual islands

Table 1 and fig.6 show that the herpetofauna of the smaller islands is much poorer than that of Soqatra. This is due to the well-known influence of both island size and habitat diversity on species numbers. Species of high altitude and a humid climate, such as *Parachalcides* and certain *Hemidactylus*, as well as arboreal *Pristurus*, are unlikely to occur on the arid satellite islands. However it should be noted that the fauna of the lesser islands has not been sufficiently explored. During a two-day

Table 1: Terrestrial reptile species known from the three main islands of the Soqotran archipelago. Non-endemic (probably allochthonous) species are denoted by an asterisk (*).

Soqotra	Semha	Abd el Kuri
Gekkonidae		
<i>Haemodracon riebecki</i> (Peters)	<i>Haemodracon</i> sp. (Joger, in prep.)	
<i>H. trachyrhinus</i> (Boulenger)		
<i>Hemidactylus flaviviridis</i> Rüppell*		<i>Hemidactylus forbesii</i> Boulenger
<i>H. granti</i> Boulenger		
<i>H. homoeolepis</i> Blanford	<i>Hemidactylus</i> , cf. <i>homoeolepis</i>	<i>H. oxyrhinus</i> Boulenger
<i>H. pumilio</i> Boulenger		
<i>H. turcicus</i> Linnaeus*		
<i>H. sp.</i> (Joger, in prep.)		
<i>Pristurus abdelkuri</i> Arnold*		<i>Pristurus abdelkuri</i> Arnold
<i>P. guichardi</i> Arnold	<i>Pristurus</i> sp. (Rösler & Wranik, in press)	
<i>P. insignis</i> Blanford		
<i>P. insignoides</i> Arnold		
<i>P. sokotranus</i> Parker		
<i>P. sp.</i> (Rösler & Wranik, in press)		
Chamaeleonidae		
<i>Chamaeleo monachus</i> Gray		
Lacertidae		
<i>Mesalina balfouri</i> (Blanford)	<i>Mesalina</i> cf. <i>balfouri</i>	<i>Mesalina</i> cf. <i>balfouri</i>
Scincidae		
<i>Mabuya socotrana</i> (Peters)	<i>Mabuya</i> cf. <i>socotrana</i>	<i>Mabuya</i> cf. <i>socotrana</i>
<i>Parachalcides sokotranus</i> Boulenger		
Trogonophidae		
<i>Pachycalamus brevis</i> Günther		
Leptotyphlopidae		
<i>Leptotyphlops filiformis</i> (Boulenger)		
<i>L. macrura</i> (Boulenger)		
Typhlopidae		
<i>Typhlops socotranus</i> Boulenger		
Colubridae		
<i>Coluber socotrae</i> (Günther)	<i>Coluber</i> cf. <i>socotrae</i>	
<i>Diityophis vivax</i> Günther		

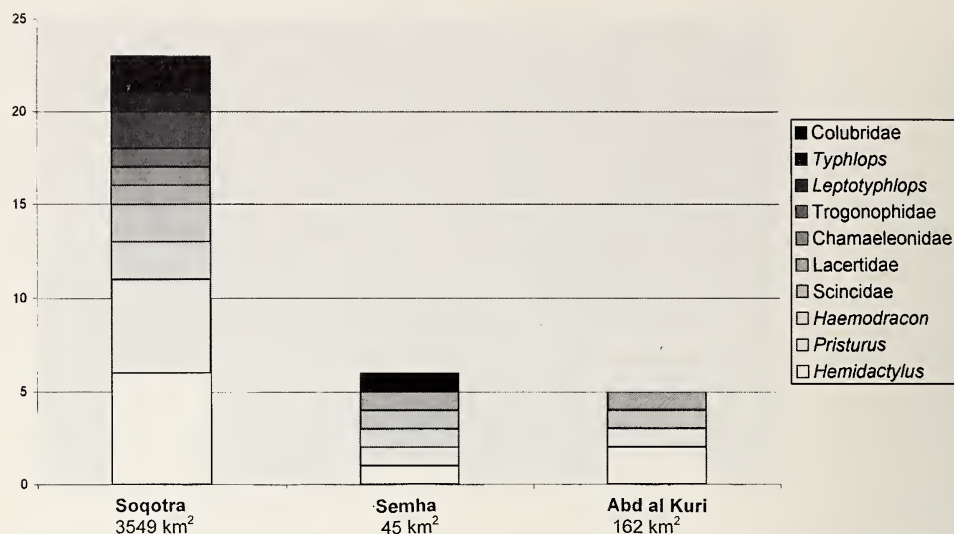


Fig. 6: Comparison of the reptile fauna of the three main islands of the Soqotran archipelago

stay on Semha, we discovered a new *Haemodracon* (fig.7) and a new *Pristurus* (fig. 8), and further taxa may have escaped our attention. For instance, the wormlike underground reptiles *Pachycalamus*, *Typhlops* and *Leptotyphlops* cannot be excluded. Other taxa, such as the *Mesalina* and *Coluber* of Semha, appear slightly different from their Soqotran congeners. Molecular investigations have been initiated to find out whether speciation has already occurred in these genera.

The reptile fauna of Abd El Kuri, the westernmost and most arid island, appears even more reduced in number of species, although its size is much larger than Semha. Nevertheless it contains three locally endemic gecko species, indicating an independent evolution as a result of long geographical isolation. Sea depth between Abd El Kuri and the other islands is more than 200 m, making any Pleistocene land connection unlikely (whereas Semha could have been connected to Soqatra via the smaller islet Darsa during times of lowest sea level).



Fig.7: *Haemodracon* sp., a new species (Joger, submitted) of leaf-toed gecko from Semha.



Fig.8: *Pristurus* sp. from Semha, described as a new species (Rösler & Wranik, submitted)

So far, no snake species have been collected on Abd El Kuri. However, we could only explore a small part of that island, and its faunal list may be not complete.

Radiations within the archipelago

Two-thirds of the reptile species of the Soqatra archipelago are geckos. Of them, two genera have undergone major radiations and multiple speciations:

- A diurnal radiation is represented by the genus *Pristurus*. The definite number of species and subspecies in the archipelago has yet to be determined, but there are at least five endemic taxa on Soqatra and one each on Semha and Abd El Kuri². Niche separation between them is mainly achieved by different microhabitats: one species is more or less ground dwelling (*P. socotranus*), two are saxicolous (*P. insignis* complex), and two are arboreal (*P. guichardi* complex).
- A nocturnal radiation is made up of *Hemidactylus* species. At least six species (three of them introduced) occur on Soqatra, one on Semha, and two on Abd El Kuri. Two Soqotran species (one of them new) are confined to the highlands. All live on rocks, but sympatric species are distinguished by size difference, so apparently occupying different food niches. A similar situation is found in the likewise nocturnal *Haemodracon*, a genus of which two species (*H. riebecki* on Soqatra and *H. sp.*, fig.7, on Semha) exceed sympatric *Hemidactylus* in size, whereas a third one (*H. trachyrhinus* on Soqatra) is very small (Rösler & Wranik).

Exploring speciation within these species complexes is an important task for future research.

²) *Pristurus abdelkuri* also occurs as an introduced population in coastal areas of Soqatra.



Fig. 9: One of many dead Green turtles (*Chelonia mydas*) near a fishermen's landing point on Abd El Kuri. Also habitat of *Hemidactylus forbesii*.

Conservation

The only reptiles that are threatened by direct human exploitation are sea turtles, which are caught by fishermen off the coast and probably also on their nesting beaches (fig.9). They are locally consumed and therefore their protection by CITES is not effective on Soqatra. Wranik (1998a) expresses concern that *Chamaeleo monachus* might be threatened by collecting for pet keepers. This fear is, however, not justified, as chameleon trade is controlled by CITES, and commercial pet traders have more accessible places elsewhere to supply themselves with chameleons. Moreover, the species is widespread and abundant on the island but difficult to find, due to its effective camouflage.

There is, however, an increasing pressure on reptile habitats by construction and development projects. Most reptiles occur in abundant numbers, but the large leaf-toed geckos of the genus *Haemodracon* appear to be less numerous and more vulnerable than other species. They lead a more or less sessile life in Dragon blood trees (*Dracaena cinnabari*) and Date palms (*Phoenix dactylifera*), but only old large trees with holes appear suitable. Tree cutting could adversely affect their populations. However they were also seen on vertical rocks with crevices. The population of the new species on Semha appears especially endangered due to its small total population size. Other potentially threatened species are those restricted to special biotopes, such as mangrove forests (*Pristurus* sp., fig.10) and higher altitude habitats (some *Hemidactylus* species, *Parachalcides socotranus*).



Fig.10: A mangrove-dwelling *Pristurus*, described as a new species (Rösler & Wranik, submitted).

An additional danger, the devastating effect of which is known from many island faunas, is introduction of foreign species. The Soqotran capital, Hadibo, is already devoid of indigenous *Hemidactylus* due to the presence of introduced *H. flaviviridis* and *H. turcicus* which have apparently outcompeted the original species. Introduced rats (*Rattus rattus*) are also very abundant at Hadibo. At present there are no dogs on the island, but if there were as many wild dogs as in mainland Yemen they would present a threat to the colubrid snakes. Cats are already abundant on Soqotra.

Conclusions

The current reptile fauna of the Soqotran archipelago is unique and results from a long evolutionary diversification of an ancient African or Afro-Arabian stock. Future studies should aim at the reconstruction of the phylogenies of these and other groups of Soqotran organisms.

A comparative estimation of genetic distances from mainland Arabian, African and Socotran taxa of several genera is in preparation. Such investigations promise to provide insights into the process of speciation, as well as into an understanding of the evolutionary and biogeographic history of East Africa, Arabia and the western Indian Ocean.

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References

- Al Sagheir, O. & R. F. Porter (1998): The bird diversity of Soqotra. – pp.199-212 in: Proceedings of the first international symposium on Soqotra island: Present and future (ed. Dumont, H.J.). – United Nations Publications, New York.
- Arnold, E.N. (1981): Recently extinct reptile faunas from southwest Indian Ocean. – BMNH Triennial Rep. 1978-80: 52-56.
- Arnold, E.N. (2000): Using fossils and phylogenies to understand evolution of reptile communities on islands. – pp. 309-323 in: Isolated Vertebrate Communities in the Tropics. Proceedings of the 4th international Symposium of the Research Institute and Zoological Museum Alexander Koenig, Bonn. (ed. Rheinwald, G.) – Bonn. zool. Monogr. 46
- Bauer, A., D.A. Good & W.R. Branch (1997): The taxonomy of the southern African leaf-toed geckos (Squamata: Gekkonidae), with a review of Old World “*Phyllodactylus*” and the description of five new genera. – Proc. Calif. Acad. Sci. 49 (14): 447-497.
- Bogert, C.M. (1940): Herpetological results of the Vernay Angola expedition. Part I, including an arrangement of the African Colubridae. – Bull. Am. Mus. Nat. Hist. 77: 1-107.
- Böhme, W., U. Joger & B. Schätti (1989): A new monitor lizard (Reptilia: Varanidae) from Yemen, with notes on ecology, phylogeny and zoogeography. – Fauna Saudi Arabia 10: 433-448.
- Boulenger, G.A. (1903): Reptiles. – pp.75-105 in: Natural History of Socotra and Abd-el-Kuri (ed. Forbes, H. O.). – Bull. Liverpool Mus. (Spec. Bull.): 75-105.
- Corkill, N.L. & J.A. Cochrane (1966): The snakes of the Arabian Peninsula and Socotra. – J. Bombay Nat. Hist. Soc. 62: 475-506.
- Dixey, F. A., M. Burr & O. Pickard-Cambridge (1898): On a collection of insects and arachnids made by Mr. E. N. Bennett in Socotra, with descriptions of new species. – Proc. Zool. Soc. London 1893: 372-391.
- Eiselt, J. (1962): Ergebnisse der zoologischen Nubien-Expedition 1962, Teil II: Amphibien und Reptilien. – Ann. Naturh. Mus. Wien 65: 281-296.
- Forbes, H.O. (1903): Natural History of Socotra and Abd-el-Kuri. – Bull. Liverpool Mus. (Spec. Bull.): 1-598.
- Girdler, R.W. (1984): The evolution of the Red Sea and the Gulf of Aden in space and time. – pp. 747-762 in: Marine Science of the North-West Indian Ocean and adjacent waters. Deep Sea Research Part A: Oceanographic research

- papers 31. Oxford.
- Günther, A. (1881): Descriptions of the amphisbaenians and ophidians collected by Prof. I. Bayley Balfour. – Proc. Zool. Soc. London 40: 461-463.
- Joger, U. (1984): The venomous snakes of the Near and Middle East. – Tübinger Atlas des Vord. Orients, Beih. A 12, 115 pp.
- Joger, U. (1985): The African gekkonine radiation – preliminary phylogenetic results, based on quantitative immunological comparisons of serum albumins. – pp. 479-494 in: Proceedings of the International Symposium on African Vertebrates (ed. Schuchmann, K.-L.). Bonn 1985.
- Joger, U. (1986): Phylogenetic analysis of *Uromastix* lizards, based on albumin immunological distances. – pp. 187-192 in: Studies in Herpetology. Societas Europaea Herpetologica (ed. Rocek, Z.). Prague.
- Joger, U. (1987): An interpretation of reptile zoogeography in Arabia, with special reference to Arabian herpetofaunal relations with Africa. – pp.257-271 in: Proceedings of the Symposium on the Fauna and Zoogeography of the Middle East, Mainz 1985 (eds. Kinzelbach, R., F. Krupp & W. Schneider): Tübinger Atlas des Vorderen Orients, Beiheft A 28.
- Joger, U. (1991): A molecular phylogeny of agamid lizards. – Copeia 1991 (3): 616-622.
- Joger, U., H. Pohl & W. Schneider (1999): Kurzbericht über eine Expedition auf das Sokotra-Archipel. – Informationen aus dem Hessischen Landesmuseum Darmstadt 99/1: 30-33.
- Klaver, C. & W. Böhme (1986): Phylogeny and classification of the Chamaeleonidae (Sauria) with special reference to hemipenis morphology. – Bonn. zool. Monogr. 22: 1-64.
- Miller, A.G. & M. Bazara'a (1998): The conservation status of the flora and fauna of the Soqotran Archipelago. – pp. 15-34 in: Proceedings of the first international symposium on Soqotra island: Present and future (ed. Dumont, H.J.). – United Nations Publications, New York.
- Parker, H. W. (1949): The snakes of Somaliland and the Sokotra islands. – Zool. Verh., Rijksmus. Natuurl. Hist. Leiden 6: 1-115.
- Peters, W. (1882): Mittheilung über die von Herrn Dr. E. Riebeck auf Socotra gesammelten Reptilien. – Sitzungsber. Ges. naturforsch. Freunde Berlin 1882: 42-46.
- Rösler, H. & W. Wranik (1998): Beiträge zur Herpetologie der Republik Jemen. 3. Geckos des südlichen Jemen und der Insel Sokotra (Reptilia: Sauria: Gekkonidae). – Faun. Abh. Staatl. Mus. Tierkde. Dresden 21: 113-132.
- Schneider, W. (1996): Sokotra – die Insel der Dioskuriden. – Informationen aus dem Hessischen Landesmuseum Darmstadt 96(1): 25-28.
- Schneider, W. & H.J. Dumont (1998): Checklist of the Dragonflies and Damselflies of Soqotra island (Insecta: Odonata). – pp. 219-232 in: Proceedings of the first international symposium on Soqotra island: Present and future (ed. Dumont, H. J.). – United Nations Publications, New York.
- Schoff, W.H. (1912): The Periplus of the Erythraean Sea. – New York.

- Steindachner, F. (1903): Batrachier und Reptilien aus Südarabien und Sokotra, gesammelt während der südarabischen Expedition der kaiserlichen Akademie der Wissenschaften. – Sitzber. Kais. Akad. Wiss. Wien, Math-nat. Kl., 112: 7-14.
- Wermuth, H. (1965): Liste der rezenten Amphibien und Reptilien. Gekkonidae, Pygopodidae, Xantusiidae. – Das Tierreich, Berlin 80.
- Wranik, W. (1998a): Faunistic notes on Soqotra island. – 135-198 in: Proceedings of the first international symposium on Soqotra island: Present and future (ed. Dumont, H. J.). – United Nations Publications, New York.
- Wranik, W. (1998b): Contributions to the herpetology of the Republic of Yemen. 4. Socotra Island and southern Yemen mainland. – Faunist. Abh. staatl. Mus. Tierk. Dresden 21/Suppl.: 163-182.
- Wranik, W., K.B. Reddy & A.R. Thabet (1986): Socotra island. Contributions to the flora and fauna. – Aden University, 150 pp.

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Preliminary chromosomal results of *Niviventer* Marshall, 1976 (Mammalia, Rodentia, Muridae) from the Dalat plateau in southern Vietnam

M.I. Baskevich & G.V. Kuznetsov

Abstract: Results of chromosomal studies (routine staining, C-banding) of 33 specimens of *Niviventer* rats collected in two localities (Cong Troi and Phi Lieng) of Dalat Plateau in Southern Vietnam are presented. The rats were identified on the basis of preliminary cranial and electrophoretic data (Likhnova et al. 1998) as *N. tenaster*, *N. fulvescens* and *N. langbianis*. All specimens have $2n=46$ chromosomes. The most distinctive was the karyotype of *N. langbianis* (1 female) collected in tropical forest at about 1000 m above sea level in Phi Lieng. The karyotypes of *N. tenaster* (21 specimens) and *N. fulvescens* (11 specimens) were similar at the level of routine staining of chromosomes, and distinctive at C-banding in heterochromatin quantity and intensity of Y-chromosome's staining. The possible role of chromosomal peculiarities in forming and supporting the isolating mechanisms among these sympatric but not syntopic species is discussed.

Key words: Chromosomes, Rodentia, Muridae, *Niviventer* rats, Dalat Plateau, Vietnam.

Introduction

Dalat Plateau is situated in Lambdong Province (southern Vietnam) where a special ecologo-faunistic group of rodents is suspected (Cao Van Sung & Kuznetsov 1992a). The distribution of the Vietnam endemic *Rattus osgoodi* at least is limited to this area. Therefore it is of interest to gain more information about the composition and distribution of rodents from this region including that of the Dalat Plateau. The data on rodents from Dalat Plateau so far are fragmentary and based only in a few cases on modern genetic approaches (Baskevich & Kuznetsov 1998, Likhnova et al. 1998).

In this report we present the results of karyological studies of *Niviventer* rats - important components of the vertebrate community in the pine and tropical forests of the Dalat Plateau.

Material and methods

The specimens were collected in December 1995 at two localities of the Dalat Plateau: Cong Troi and Phi Lieng. The 33 specimens were identified on the basis of preliminary cranial and electrophoretic data (Likhnova et al. 1998) as *N. tenaster*, *N. fulvescens* and *N. langbianis*. Preparations of mitotic chromosomes were obtained by means of the general air-drying technique. The C-banding staining procedure was carried out according to Sumner (1972).

Results

The most distinctive was the karyotype of *N. langbianis* (one female, collected in tropical forest at about 1000 m above sea level in Phi Lieng). Its $2n=46$ -karyotype consists of one pair of large subtelocentric, 18 pairs of acrocentric, three pairs of small metacentric autosomes and acrocentric X-chromosomes. At C-band-staining small pericentromeric heterochromatin blocks were distinguished in almost all autosomes and X-chromosomes (fig. 1). The karyotype of this endemic to Indochina is studied here for the first time. It is noteworthy that on the level of routine staining its karyotype is close to that of *N. cremoviventer*, described earlier from the Malay Peninsula (Yong 1969a) and from Tai-Nguen Plateau in Vietnam (Chan Van Minh 1988). This may point to close phylogenetic relationships between these two species on the South-East Asian mainland. On the other hand it is known that the karyotype of *N. cremoviventer* of the Sunda Shelf (Java) has a specific karyotype ($2n=46$, $NF=60$) (Duncan et al. 1974). This last fact may demonstrate the effect of long geographical isolation on the chromosomal differentiation of *Niviventer* rats.

The $2n=46$ -karyotypes of *N. tenaster* (21 specimens) and *N. fulvescens* (11 specimens) are similar on the level of routine staining of chromosomes: the karyotypes are composed of 19 pairs of gradually decreased acrocentric and three small pairs of metacentric autosomes, medium-sized submetacentric X- and small acrocentric Y-chromosomes. At C-band-staining one can observe significant interspecific differences between their chromosomal sets. In *N. tenaster*, large strongly stained heterochromatin blocks were observed in all autosomes. The medium-sized X-chromosome has an additional heterochromatin in the short arm, the Y-chromosome is fully heterochromatinized, but the intensity of its hetero-

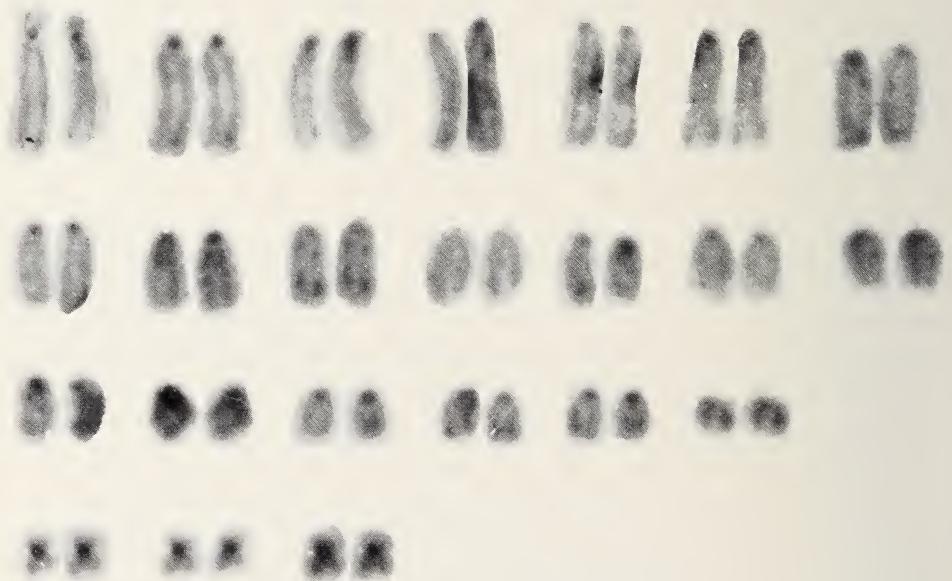


Fig. 1: C-band-stained karyotype of female *Niviventer langbianis* from Phi Lieng

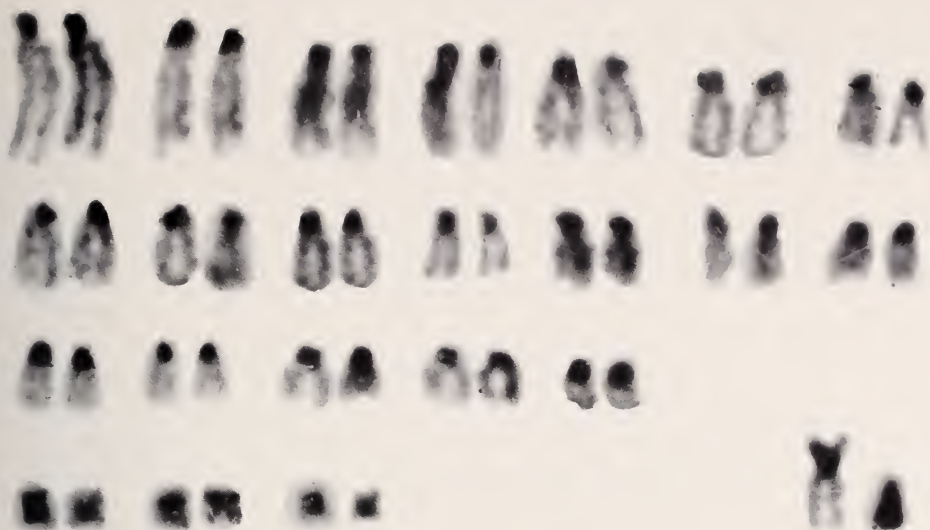


Fig.2: C-band-stained karyotype of male *N. tenaster* from tropical forest in Cong Troi

chromatin staining is less than that of the autosomes (fig.2). Using C-band-staining in the karyotype of *N. fulvescens* (fig.3), however, only small, mainly slightly stained heterochromatine blocks of pericentromeric localization in all the autosomes, that of intercalaric localization in a few autosomes, and more intensively stained heterochromatin of heterochromosomes were revealed.

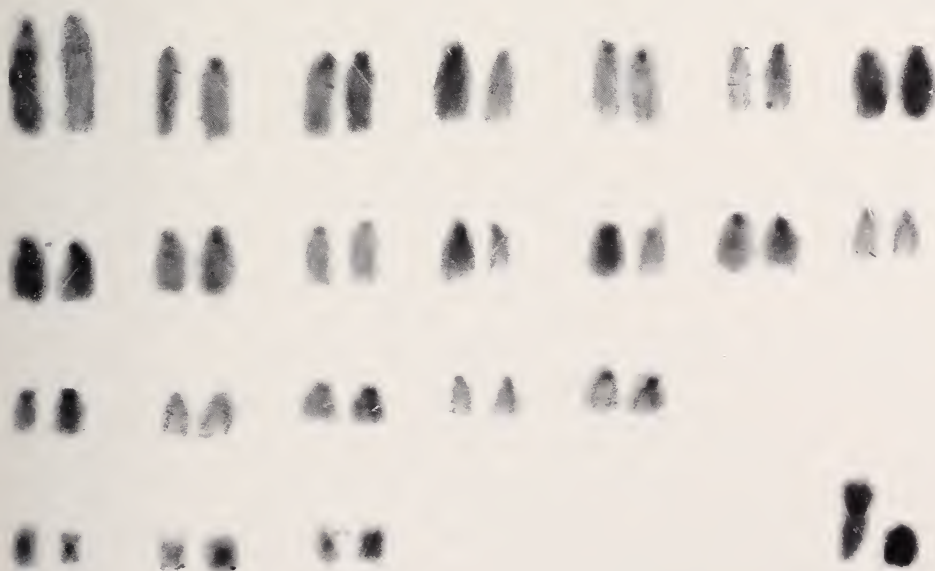


Fig.3: C-band-stained karyotype of male *N. fulvescens* from pine forest of Phi Lieng

Discussion

When we compare our results we can say that the chromosomal peculiarities, in addition to morphological and electrophoretic ones (Likhnova et al. 1998), allow us to distinguish these three sympatric but not syntopic *Niviventer* species in Dalat Plateau. They are not syntopic because all studied specimens of *N. tenaster* were collected in tropical forest at 1600 m a.s.l. in Cong Troi, whereas all specimens of *N. fulvescens* were collected in pine forest at both localities (Phi Lieng and Cong Troi) of the Dalat Plateau. *N. langbianis* on the other hand belongs to the arboreal habitus type; the single female of this species was trapped by us in the tropical forest in Phi Lieng, so we can see a clearly expressed biotopic isolation between these three sympatric *Niviventer* species in Dalat Plateau.

N. longbianis and *N. tenaster* are Indochinese endemics while *N. fulvescens* has a wider distribution (it is the only member of the genus with a geographic distribution encompassing the SE Asian mainland and some islands of the Sunda Shelf; Musser 1981, Musser & Carleton 1993). It is obvious that the ranges of the three species overlap to some degree. Therefore it is of interest to study their isolation mechanisms on various levels (ecological, chromosomal and others). We believe that chromosomal peculiarities do not play an important role in forming and supporting the isolating mechanisms among these sympatric but not syntopic species because interpopulational chromosomal variability was marked in the widely distributed *N. fulvescens* (Yong 1969a,b, Duncan et al. 1970, 1974, Markvong et al. 1973, Cao & Chan 1984, Cao & Kuznetsov 1992, our data). The high variability may indicate the taxonomical complexity of *N. fulvescens*.

Table 1: Chromosome variability in populations of *Niviventer fulvescens*

Country, locality	2n	Autosomes (pairs)				Sex chromosomes		NF	Reference
		M	S M	ST	A	X	Y		
Vietnam, Con Son Is.	46	3	0	1	18	A	A	54	Duncan et al. 1970
Vietnam, Dalat Plateau	46	3	0	0	19	SM	A	54	our data
Vietnam	46	3	0	4	15	A	A	60	Cao & Chan 1984
Vietnam	46	3	0	4	15	SM	A	60	Cao & Kuznetsov 1992b
Thailand	46	3	0	4	15	A	A	60	Yosida 1973
Thailand	46	3	0	1	18	A	A	54	Markvong et al. 1973
Malaja	46	3	0	1	18	A	A	54	Yong 1969a
Java	46	3	0	4	15	A	A	60	Duncan et al. 1974
Hong Kong	46	3	0	4	15	ST	A	61-o 60-o	Yong 1969b

Notes: 2n = diploid number of chromosomes, NF = fundamental number, M = metacentric, SM = submetacentric, ST = subtelocentric, A = acrocentric

On the other hand it is known that the heterochromatin quantity can have an effect on the behavior of chromosomes at the meiotic prophase (Borodin et al. 1995). The positive correlation between the heterochromatin quantity and the asinapsis of heterochromosomes at the meiotic prophase may support the idea of possible contributions of chromosomal peculiarities to the forming and support of isolation mechanisms between these sympatric *Niviventer* species whose karyotypes are characteristic in their different heterochromatin patterns.

The results obtained allow us to discuss the phylogenetic relationships between the *Niviventer* taxa on a new basis. Our data support the division of *Niviventer* suggested earlier by Musser (1981) and which was based recently on electrophoretic results (Likhnova et al. 1998).

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References

- Baskevich, M.I. & G.V. Kuznetsov (1998): To the question of cytogenetic differentiation of the *Rattus* rats (Rodentia, Muridae) from the Dalat Plateau in South Vietnam. – Zool. Zhurn. 77: 1521-1528.
- Borodin, P.M., O.V. Sablina & M.I. Rodionova (1995): Pattern of X-Y chromosome pairing in microtine rodents. – Hereditas 123: 17-23.
- Cao, Van Sung & Van Minh Chan (1984): Karyotypes et systematique des rats (genre *Rattus* Fischer) du Vietnam. – Mammalia 48: 557-564.
- Cao, Van Sung & G.V. Kuznetsov (1992a): About ecological and faunistic groups of rodents in the fauna of Vietnam. – pp. 198-204 in: Zoological studies in Vietnam (ed. Sokolov, V.E.). – Nauka, Moscow.
- Cao, Van Sung & G.V. Kuznetsov (1992b): About the taxonomic position of the rats of the genus *Rattus* (Muridae, Mammalia) in Vietnam. – pp. 74-81 in: Zoological studies in Vietnam (ed. Sokolov, V.E.). – Nauka, Moscow.
- Chan, Van Minh (1988): Fauna and ecological peculiarities of rodents from plateau Tai-Nguen, 22pp. – Abstract of Thesis, Moscow.
- Duncan, J.F., F.D. van Peenen & P.F. Ryan (1970): Somatic chromosomes of eight mammals from Con Son Island, South Vietnam. – Caryologica 23: 173-181.
- Duncan, J.F., R. Irsiana & A. Chang (1974): Karyotypes of five taxa of *Rattus* (Rodentia, Muridae) from Indonesia. – Cytologia 39: 295-302.
- Likhnova, O.P., G. Musser, G. Kuznetsov & J. Pavlinov (1998): Preliminary results of allozymic and cranial analyses of *Niviventer* (Rodentia: Muridae) from Southern Vietnam. – p.356 in: Abstracts of Euro-American Mammal Congress (ed. Santiago Reig). – Univ. Press, Santiago de Compostela.
- Markvong, A., J.T. Marshall, jr. & A. Gropp (1973): Chromosomes of

rats and mice of Tailand. – Nat. Hist. Bull. Siam. Soc. 25: 23-40.

Musser, G.G. (1981): Results of the Archbold expeditions (no. 105): Notes on systematics of Indo-Malayan murid rodents, and description of new genera and species from Ceylon, Sulawesi, and Philippines. – Bull. Mus. Nat. Hist. 168: 229-334.

Musser, G.G. & D. Carleton (1993): Family Muridae. – pp.501-755 in: Mammal species of the world. A taxonomic and geographic reference. 2. edit. /eds: Wilson, D.E. & D.M. Reeder). – Smithsonian Institution Press, Washington & London.

Sumner, A.T. (1972): A simple technique for demonstrating centromeric heterochromatin. – Exp. Cell Res. 75:304-306.

Yong, H.S. (1969a): Karyotypes of Malay rats (Rodentia, Muridae, genus *Rattus* Fischer). – Chromosoma 34: 245-267.

Yong, H.S. (1969b): Karyotypes of three species of rats from Hong Kong and Tailand (Muridae, genus *Rattus* Fischer). – Cytologia 34: 394-398.

Yosida, T.H. (1973): Evolution of karyotypes and differentiation in 13 *Rattus* species. – Chromosoma 40: 285-297.

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Mammals of coastal islands of Vietnam: zoogeographical and ecological aspects

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Abstract: The faunistic composition of the coastal islands of Vietnam changes according to their geographic position and landscape conditions. For example, along the 1500 km from north to south different species of *Callosciurus* can be found on the islands: Dangkho is inhabited by *C. erythraeus*, Cham by *C. flavimanus*, and the southern islands by *C. finlaysonii* with different subspecies. Similar successions and relations were reported in birds, reptiles, insects and other groups of animals. The number of individuals of the genus *Callosciurus* changes accordingly: it decreases from south to north. Obviously the environmental conditions for squirrels improve towards the south. The islands have higher numbers of mammals, chiefly of rodents, than the continent. For instance, the total number of all species of rats in natural biotopes on the islands is about twice as high as on the continent in the natural communities of primary tropical forests. A similar rule is observed among species of squirrels of the genus *Callosciurus*. The numbers of rats, however, on different islands varied from 0.9 to 10.0 per 100 trap-nights. We did not find any clear correlation between the species diversity of rats and their abundance.

Key words: coastal islands of Vietnam, mammals, diversity, ecology, biogeography

Introduction

It is noteworthy that zoologists and biogeographers find it particularly interesting to examine oceanic islands, regarding them as the simplest and most convenient models of ecological relationships between animals as well as their evolution (Voronov 1976, Chernov 1982, Guilleume 1983, Mein 1983, Yes'kov 1984, Lawlor 1986). At the same time, studies of coastal islands allow a more detailed tracing of colonization, extinction, immigration, as well as of changes in the structure of communities, when compared with the continental fauna. Such studies also help to test various hypotheses on the initial formation of insular faunas (Crowell 1986, Istomin 1989).

It is also of interest to clarify peculiarities of species diversity and to design models of the colonization of such islands by continental species. Most likely such studies were primarily driven by the concept of equilibrium zoogeography which was advanced by MacArthur & Wilson (1967) over 30 years ago. Their theory demonstrates the dynamic pattern of equilibrium in insular biota between immigration from sources of colonization and the extinction of colonists. Terrestrial mammals have specific features that are useful in colonizing islands and in distributing over them. There are also characteristic traits in the adaptational

evolution of mammals remaining on such islands because of their sudden isolation from other animals.

In this connection the study of mammals on the coastal islands of Vietnam is interesting. This is even more important because practically no theriological studies of these islands had ever been made. It should be mentioned that insular fauna is usually approached from both ecological and biogeographical points of view (Levushkin 1982).

Material and methods

We collected our materials when working within the Zoogeographical Team of the Research Vessel "Academician Aleksander Nesmeyanov". The aim was to study the insular ecosystems of the coastal shelf of Vietnam from the Archipelago of Bai Tu Long in the Gulf of Tonkin down to the islands in the Gulf of Siam. In total, we examined seven islands (Dangkho, Phoung Hoang, Cham, Bai Canh, Con Dao, Thô Chu', Thom) during the period from 20.03. to 13.04.1987. We processed 1860 trap-nights and determined the numbers of squirrels of the genus *Callosciurus*; all transect censuses equaled 65 km. By shooting, Gero traps and nets we collected about 200 individuals, chiefly Chiroptera, rats and squirrels.

Our main purpose was the study of the taxonomy of the mammalian fauna of the islands examined. We also recorded some ecological parameters of the populations of rats and squirrels (abundance, diurnal activity, distribution in the habitat, reproduction, etc.).

For other islands of the Vietnam shelf (Kaitien, Ban Sen, Quan Lan, Cat Ba and Phu Quoc) we used material from the expedition carried out by the National Central Research Institute of Vietnam during the period 1988-1998. We also considered literature relevant to this region (Kloss 1926, Van Peenen et al. 1970, Kuznetsov & Fam Chong An' 1992) and investigated mammalian collections in different museums of Vietnam, the Moscow State University and the private collection of Fam Chong An'.

Taxonomic list of mammalian species on the coastal islands of Vietnam

To characterize mammalian fauna on the coastal islands of Vietnam we used data from 12 islands: from the Archipelago of Bai Tu Long in the Gulf of Tonkin in the north to the Thô Chu' island in the Gulf of Siam in the south, i.e. we considered almost the entire area of large coastal islands of Vietnam. We identified 78 mammalian forms inhabiting the coastal islands of Vietnam obtained by trapping, direct observations, life records, and questionnaires.

The coastal islands of Vietnam are inhabited by representatives of almost all mammalian orders. On the islands of the Archipelago of Bai Tu Long in the Gulf of Tonkin small bats (*Hipposideros*, *Rhinolophus*, *Pipistrellus*, *Scotophilus*) are most numerous; among monkeys the most frequent species is *Macaca mulatta*, among rodents *Rattus*, *Niviventer*, *Leopoldamys*; among squirrels *Callosciurus*, *Tamiops*; among Carnivora *Viverricula indica*, *Prionailurus bengalensis*, *Lutra lutra*; among

Ungulata *Sus scrofa* and *Muntiacus muntjak*. *Cervus unicolor* was widespread on the islands of Bai Tu Long.

Immigration from the continent may have started on the northern islands of Vietnam, the Archipelago of Bai Tu Long; here potential ecological conditions permitted the new species to exist. However, there is no doubt that in the historical past ungulates also inhabited many southern islands of the country. Until recently, the island of Con Dao was inhabited by such a large species as *Bubalus bubalis* and the Bai Tu Long Archipelago was inhabited by mammalian species which are typical of the mainland of northern Vietnam, meaning some species have survived better on the islands than on the mainland. For example, the island of Cat Ba is inhabited by such species as *Capricornis sumatraensis*, *Macaca arctoides*, *Presbytis francoisi*. We must admit that the habitat is of greatest importance for the formation of the fauna on these islands

Chernov (1982) was right in saying that the processes of colonization of these islands are essentially determined by biological relationships and by the specific insular habitats. To illustrate this idea we can point to the habitat of *Capricornis sumatraensis* on Cat Ba: this species could survive only due to the hard rocky biotopes of the local limestone mountains. Indeed, as Chernov says, "...the essence of the question is not how it may come to the island but how it can live on it" (Chernov 1982: 36). This remark is valid for other continental islands as well.

Therefore biogeographical and ecological factors determine the distribution of many animal groups on the islands. Of particular interest in terms of mammals is the distribution of Viverridae on the coastal islands of Vietnam. Arboreal viverrid species seem to be absent from the northern islands, but quite common on some southern ones (Con Dao island). Viverrid species with a broader nutritional specialization, for instance *Viverricula indica*, have some advantages over narrow-diet viverrids widespread in terrestrial biotopes including the sea coast, while *V. indica* is spread over many islands of the Bai Tu Long Archipelago. On some of them (Kaitien, Phoung Hoang) the species is quite common. It is interesting that *V. indica* is less numerous in areas with other carnivores, for instance on Cat Ba island where *Herpestes javanicus*, *Viverra zibetha* and *Melogale moschata* live. By contrast, on the islands without competition from other carnivores, *Viverricula indica* largely increases its population (on Kaitien island). The human influence has proved to be the most powerful today in its impact upon the distribution and spread of viverrid species on the coastal islands of Vietnam.

It is likely that anthropogenic factors also explain the lack of viverrids on the island of Thom in the Gulf of Siam. Immigration of some viverrid species from the island of Phu Quoc seems possible, since the distance between these two islands is only 4 km. The same factor may explain the absence of *Hylopetes lepidus* on the island of Thom, because this island is very small and, instead of tropical forest, bears large plantations of mango and other crops, preventing *Hylopetes lepidus* from recolonizing the island (pers. comm. Cao Van Sung).

Analysis of the distribution of various animals on the islands - mammals (including bats, see table 1), reptiles, locusts, beetles and other insects - shows that we can divide them into two groups: the Archipelago of Bai Tu Long in the north

and the other islands (Darevskii et al. 1991). The principal zoogeographical border on the islands coincides with that on the mainland of Vietnam (fig.1), drawn somewhat north of Da Nang (Dao Van Tien 1978). Though the climatic regimes differ essentially, the coincidence of borders points to the predominant influence exerted by the neighbouring land upon the composition of the insular faunas, and hence to the great role animal migrations play here.

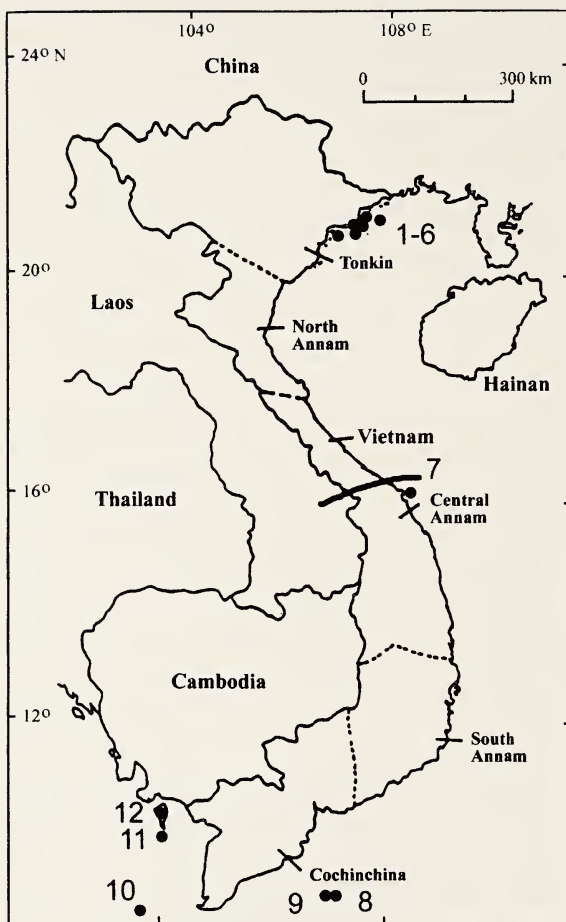


Fig.1: Map of Vietnam with the sites of studied islands:

- 1 – Kaitien
- 2 – Dangkho
- 3 – Ban Sen
- 4 – Quan Lan
- 5 – Phoung Hoang
- 6 – Cat Ba
- 7 – Cham
- 8 – Bai Canh
- 9 – Con Dao
- 10 – Tho Chu
- 11 – Thom
- 12 – Phu Quoc

Insular faunas result from a balance between immigration and extinction; the proximity to the coast does not determine any specific insular animal populations. The chiefly continental pattern of the fauna could be associated not only with the relatively late (Late Pleistocene) separation of the islands from the mainland but also with the animals' considerable migration ability. Immigration could be a reason behind the patchy pattern of many populations on the islands, but the picture observed today can be better explained by the theory of "equilibrium" insular biogeography (Darevskii et al. 1991).

Table 1: Primary list of mammals of the continental islands of Vietnam

Species	1	2	3	4	5	6	7	8	9	10	11	12
<i>Crocodylus porosus</i>	+L		+L	+L					+L			
<i>Suncus murinus</i>								+C	+L			
<i>Tupaia glis</i>	+L		+L			+L		+C	+LV			
<i>Cynopterus sphinx</i>		+L				+L						
<i>Macroglossus minimus</i>									+CL			
<i>Pteropus hypomelanus</i>								++V	++LV	+V	+V	+V
<i>P. vampyrus</i>								++V	++V	++V	+V	++L
<i>Rousettus leschenaulti</i>						+V						
<i>Taphozous melanopogon</i>						+V			+P			
<i>Megaderma spasma</i>									+L		+V	+P
<i>Hipposideros armiger</i>	+L	++V	++L	+L	++C V	++V	+V		++C V			
<i>H. bicolor</i>		+V			+V	++C	+V		+L		+CL	++L
<i>H. diadema</i>								+V	+V			+P
<i>H. larvatus</i>		++V			++C	++CL	+V	+V	++CL		+C	
<i>Rhinolophus borneensis</i>									+VL	+V		
<i>R. luctus</i>									+LV			
<i>R. thomasi</i>		+V			+V				+L			
<i>Pipistrellus abramus</i>		+V				+V						
<i>P. ceylonicus</i>							+V					
<i>P. javanicus</i>							+V					
<i>Scotophilus heathi</i>						+V						
<i>Macaca arctoides</i>			+L			+L						
<i>M. mulatta</i>	+V	++C	++C	+V	+V	++CL						
<i>M. nemestrina</i>						+L						
<i>M. fascicularis</i>							++V	++V	++VL	++V		++L
<i>Presbytis francoisi poliocephalus</i>						++CL						
<i>Hylobates lar</i>												+L
<i>Lutra lutra</i>	++V	+V	++V	+V	++C	+L						
<i>Aonyx cinerea</i>	+P											
<i>Melogale moschata</i>						+L						
<i>Paradoxurus hermaphroditus</i>	+P								++VP			+L
<i>Viverricula indica</i>	+++C	+V	++C	++C	+C	++CL			+V			
<i>Viverra zibetha</i>	+P		+P			+VL						
<i>Herpestes urva</i>		+L			+P							
<i>H. javanicus</i>						+V						
<i>Prionailurus bengalensis</i>	+C	+C			+L	+L						
<i>Panthera pardus</i>						+L						
<i>Capricornis sumatraensis</i>		+P	++V		+P	++VL						
<i>Sus scrofa</i>	++V	++C	++V	+V	++V	+V						
<i>Cervus unicolor</i>		+C				+L						
<i>Muntiacus muntjak</i>	+V	++C	++C	++V	++C	++VL						
<i>Bubalus bubalis</i>									+L			
<i>Manis pentadactyla</i>	+V	+P				+P						
<i>Callosiurus erythraeus castaneiventris</i>	++C	++C	++C	+C	++V	++C						

Species	1	2	3	4	5	6	7	8	9	10	11	12
<i>C. flavinanus</i>							++V					
<i>C. finlaysonii germaini</i>								++V	+++C			
<i>C. finlaysonii pierrei</i>												+L
<i>C. finlaysonii harmandi</i>										+++C		
<i>Dremomys rufigenis</i>						+L						
<i>Tamias maclellandi</i>	+V	+C	+V		+V	+C						
<i>Tamias swinhoei</i>						+L						
<i>Rattus bicolor hainana</i>			+V			++C						
<i>R. bicolor condorensis</i>									++C			
<i>Hylopetes spadiceus</i>									+LC			+L
<i>H. lepidus</i>												+LP
<i>Menetes berdmorei</i>											+++C	++L
<i>Rhizomys pruinosus</i>	+V	+V				+L						
<i>Bandicota indica</i>						+L						
<i>Berylmys berdmorei</i>									+L			
<i>Leopoldamys sabanus</i>						++C		++C	++C	++C		
<i>Maxomys surifer</i>											+++C	++L
<i>Mus caroli</i>						+L						
<i>Niviventer bukit</i>			++C			+L			+V	+C		
<i>N. confucianus</i>			+C									
<i>N. cremoriventer</i>			+CV		+C	+L						
<i>N. niviventer</i>			++C						+CL			
<i>N. fulvescens</i>												++L
<i>Rattus argentiventer</i>							+C			+CV		
<i>R. exulans</i>									+LC	+L		
<i>R. nitidus</i>							++C			+LC		
<i>R. norvegicus</i>		++V					++C					
<i>R. molliculus</i>		++C					++C		+LC	+++C		
<i>R. koratensis</i>						+L	++C			++C		+LV
<i>R. flavipectus</i>	+++C			+++C	++C							
<i>R. germaini</i>							+C	++C	+VC	++C		
<i>Hystrix brachyura</i>	+V	+V	+V		++V	+L						
<i>Atherurus macrourus</i>						+LC						
<i>Lepus peguensis</i>									+CL			

Legend

1 – 12: names of the islands: 1 – Kaitien; 2 – Dangkho; 3 – Ban Sen; 4 – Quan Lan; 5 – Phoung Hoang; 6 – Cat Ba; 7 – Cham; 8 – Bai Canh; 9 – Con Dao; 10 – Thô Chu'; 11 – Thom; 12 – Phu Quoc.

+ – rare species, ++ – uncommon species, +++ – common species, C – the species was collected.

L – published data, V – visual observations, P – information by local people.

Ecological peculiarities and the evolution of insular mammals

The mammals of the coastal islands of Vietnam illustrate some of the ecological regularities of insular biogeography. For example, on some islands (Cham, Thô Chu') we found a compensation effect, i.e., when the diversity of rat species on an island decreases, the number of individuals increases. However, this effect was not manifested in all cases, suggesting more intricate relations in multi-species communities. Obviously, the mechanisms governing the

formation of insular communities are still unclear. The hypothesis has been advanced that during the succession of insular invertebrate faunas, “early” species with high reproduction rates are replaced by “late” species with low reproduction rates. In terms of population ecology this can be explained by the turnover from r-strategy to K-strategy, and by the increasing complexity in the trophic structure of the community. In terms of biogeography this can be explained by the growing importance of the “late” species with their slower rates of colonization (Sukhanov 1982: 74). It is possible that to some extent mammals use the same strategy.

However, there are no reliable data on the variations in the species composition of every insular fauna type, making it difficult to apply this hypothesis to all mammal species. It is obvious, however, that in all species of different genera of rats dispersion plays an important role. According to the studies of Kucheruk & Lapshov (1989) - using “competitiveness” among representatives of local *Rattus* species as a factor in distribution - we can explain the poor penetration of the Brown rat into many islands between South-East Asia and Australia. In our analysis *Rattus norvegicus* was caught on the island of Cham not far from the port of Da Nang in the central part of Vietnam. Except for sightings on Dangkho, this species was not found on the other islands.

Half of the islands studied are inhabited by 6 to 7 rat species (except the islands of Kaitien, Ban Sen and Quan Lan where rats were not studied). On the different islands different species are dominant: on Dangkho 72% of all rats caught are *Rattus flavipectus*, on Cham the most abundant is *R. nitidus* (42.1%), prior to *R. norvegicus* (26.3%). On the southern islands other species are predominant. Among the dominants on Con Dao we found *Leopoldamys sabanus* (66,6%); on Bai Canh *R. germaini* (55.5%) and *L. sabanus* (33%); on Thom *Maxomys surifer* (100%); on Thô Chu *R. koratensis* (42.1%) and *R. germaini* (26.3%). Taking into account the predominant colonization of small islands by the House mouse *Mus musculus* (Kucheruk & Lapshov 1989), mice of the genus *Mus* must undoubtedly be present on many coastal islands of Vietnam. However, only *Mus caroli* has so far been recorded, solely on Cat Ba.

There are considerable differences in population numbers of rats between different islands, caused mainly by human influence on the natural ecosystems of the islands. These impacts enhance the reproduction of the most competitive species of rats, which are well adapted to changes in the local climatic conditions and habitats.

Despite the generally low altitudes of the islands (the maximum height above sea level is 600 m), many of them exhibit altitudinal differentiation in mammalian populations. For example on Dangkho (the highest site above sea level is 140 m), the mammalian population is altitudinally differentiated both in terms of species and numbers. The maximum population density among rats, mainly *Rattus flavipectus* (72% of all individuals), was registered at the coast near human dwellings (26.6 individuals per 100 trap-nights) and in anthropogenic landscapes (5.3 individuals per 100 trap-nights) up to the altitude of 20 m a.s.l. Above that height the plant communities, and accordingly the rat species, undergo a successional change. *Callosciurus erythraeus*, *Macaca mulatta* and *Niviventer bukit* inhabit the tropical forest from 60 to 140 m a.s.l., i.e. the upper part of the island. *Muntiacus muntjak* and *Cervus unicolor* are encountered in almost all biotopes of the island, except its rocky coast and the narrow anthropogenic zone. *Lutra lutra* colonizes only the marine coastal zone, feeding on marine invertebrates (mollusks, crabs, etc.), up to 2 m a.s.l. *Viverricula indica* and *Prionailurus bengalensis* are more frequently found on the sea coast, but sometimes also on mountain slopes. A strict vertical zonation was found in the distribution of the herpetofauna, for instance on the island of Con Dao (pers. comm. I.S. Darevskii).

According to geographical position and landscape conditions, some specific altitudinal distribution patterns of mammals were also observed on the other islands studied, such as Con Dao, Bai Canh, and Thô Chu'. Their animal populations change from north to south (from the Gulf of Tongking to the Gulf of Siam). Along the more than 1500 km of islands we find a succession of species of the genus *Callosciurus*. Dangkho is inhabited by *C. erythraeus*, Cham by *C. flavimanus*, and the southern islands by *C. finlaysonii* with different subspecies. This succession may be related to some peculiarities of zoogeographical regions on the mainland. A similar succession and relationship were found in birds, reptiles, insects and other groups of animals.

Squirrels of the genus *Callosciurus* occur on the southern islands in greater numbers (e.g., 2.16 individuals per km of census on Thô Chu') than on the northern ones (e.g., 0.77 individuals per km on Dangkho). Apparently the south offers a more favorable environment for squirrels, permitting them to realize their biotic potential.

Compared to the mainland, the islands have higher numbers of mammals, mainly of rodents. For instance, the total numbers of all rat species in natural habitats on the islands are about twice as high as in primary tropical forests on the mainland of Vietnam. A similar relationship can be observed among species of *Callosciurus* squirrels. With the number of rats on different islands varying from 0.9 to 10.0 trap-nights, we did not find any correlation between the diversity of rats and their abundance. This shows that the numbers of individual animals and their species numbers are formed by complex mechanisms. It is possible that a certain role in the process is played by the size of an island and its habitat diversity. It is interesting that the highest numbers of rats were recorded on Cham and Thô Chu', with areas of 11.9 - 13.8 km².

On small islands we noted the phenomenon of "faunistic deficiency". This can be accounted for by the fact that the area of such islands - as a rule - is smaller than the critical territory necessary for certain species of mammals, birds or other groups of animals. At the same time, these islands are under heavy human pressure (Cham, Thom, Thô Chu'). Insular ecosystems are known to be less resistant to anthropogenic impacts than continental ones.

However, there are cases when "faunistic deficiency" can be largely attributed to other reasons, such as ecological or landscape factors (habitat equipment, terrain features, lack of water bodies, etc.) or isolation by strong sea currents between islands. The latter is the case between Con Dao and Bai Canh, where straits of just 800 m in width separate the islands, thus forming a barrier for many animals. This is obviously the reason why the mammalian fauna on Bai Canh is 1.5 to 2 times poorer than that on Con Dao. Since this also applies to the insect fauna (pers. comm. A. Ponomarenko), the diversity of ants on Bai Canh is much lower than on the island of Con Dao. However, there are some ant species which are found only on Bai Canh. Therefore the difference in the faunistic composition cannot be explained by the different size of the islands alone. The presence of different species on Bai Canh and on Con Dao favors the suggestion that their fauna is rather transient, which corresponds to the predictions of the equilibrium theory of insular biogeography.

On the other hand, the essentially lower diversity of animals on Bai Canh island compared with Con Dao, despite the anthropogenically impoverished fauna of the latter, points to the primary significance of the dimensions of islands and also favors the theory of equilibrium biogeography.

Habitat equipment does not only influence the colonization process on the islands (Chernov 1982) but also the survival of the species there. It governs the conditions of habitat diversity the moment the islands become isolated and then maintains this diversity of plant communities. We believe that this can be demonstrated by the existence of *Lepus peguensis* (a xerophilous

species) on Con Dao, or of some strictly specialized species (such as *Tupaia*) inhabiting the tropical forest on Bai Canh, or *Capricornis sumatraensis* living on the limestone residual rocks of Cat Ba. At the same time isolation of the islands promoted the divergence of various groups of animals. So, the mammalian fauna on the coastal islands of Vietnam characteristically contains endemics of mainly subspecies rank. For example, on Con Dao more than 13 subspecies of mammals were recorded. We find similar examples in birds and reptiles. All this demonstrates the rate of insular divergence within the last 10 - 15 thousand years. Today the rate of mammal diversification on the coastal islands is basically limited by the rate of extinction (Lawlor 1986).

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References

- Chernov, Yu. I. (1982) : On the ways and sources for the formation of fauna of small islands in the Oceania. – Zhurn. obshch. biol. 43: 35-47.
- Crowell, K.L. (1986) : A comparison of relict versus equilibrium models for insular mammals of the Gulf of Maine. – Biol. J. Linn. Soc. 28: 37-64.
- Dao Van Tien (1978) : An experience in zoogeographical regionalisation of Vietnam. – Zool. zhurn. 57: 582-586.
- Darevskii, I.S., A.G. Ponomarenko & G.V. Kuznetsov (1991): Zoogeography of coastal islands of Vietnam. – Priroda 9: 42-48.
- Guilleume, C.P. (1983): Les reptiles insulaires mise en place et evolution. – Colloq. Intern. CNRS 330: 281-287.
- Heaney, L.R. (1986): Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. – Biol. J. Linn. Soc. 28: 127-165.
- Istomin, A.V. (1989) : Formation of insular communities and populations as illustrated by the example of small mammals from the Kandalaksha Bay of White Sea. – Author. abstr. dissert. : p. 21.
- Kloss, C.B. (1926) : Mammals from Pulo Condore, with descriptions of two new subspecies. – J. Nat. Hist. Soc. Siam 4 : 357-359.
- Kucheruk, V.V. & A.V. Lashov (1989) : Synanthropic rodents of oceanic islands. – Ekologia 2: 41-49.
- Kuznetsov, G.V. & Fam Chong An' (1992) : Mammals of the coastal islands of Vietnam (biogeographical and ecological aspects). – pp. 182-197 in: Zoological investigations in Vietnam (ed. Sokolov, V.E.). – Moscow, Nauka.
- Lawlor, T.E. (1986) : Comparative biogeography of mammals on islands. – Biol. J. Linn. Soc. 28: 99-125.
- Levushkin, S.N. (1982). : The problem of insular faunas in the light of relations between biogeography and ecology. – pp. 26-52 in : Morskaya biogeog. : predmet, meth., printsipy raionir. – Moscow, Nauka.
- MacArthur, R.H. & E.O. Wilson (1967) : The theory of island biogeography. – Princeton, Univ. Press.

- Mein, P. (1983) : Particularités de l'évolution insulaire chez les petits mammifères. – Colloq. intern. CNRS 330: 189-193.
- Sukhanov, V. V. (1982) : A model of species abundance distribution over the littoral of an insular ridge. – pp. 52-75 in: Morskaya biogeog. : predmet, meth., printsipy raionir. – Moscow, Nauka (1982).
- Van Peenen, P.F., M.L. Cunningham & J.F. Duncan (1970) : A collection of mammals from Con Son island, Vietnam. – J. Mammal. 51: 419-424.
- Voronov, A.G. (1976) : General problems of biogeography and its main trends at the present-day stage. – pp. 8-97 in: Itogi nauki i tekhniki. Biogeografiya. – Moscow. VINITI (1978).
- Yes'kov, K.Y. (1984): The drift of continents and problems of historic biogeography. – pp. 24-92 in: Faunagenesis and phylogenesis (ed. Chernov, Y.I.). – Nauka, Moscow.

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On the herpetofauna of the Sultanate of Oman, with comments on the relationship between the Afrotropical and Saharo-Sindian faunas

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Abstract: At present a total of 90 species of amphibians and reptiles is known to occur in the Sultanate of Oman. During a field trip to the Sultanate a total number of 272 specimens representing 32 species of reptiles and amphibians was collected. Six additional species were observed but not collected. Some recently collected material, comprising 16 species and 30 specimens from the ZFMK collection, is included in the commented list provided, resulting in a total of 42 species listed. It is followed by a list of localities visited with their respective herpetofaunal communities.

The zoogeographic relationships of the Omani herpetofauna with the Palearctic (Iran) and Afrotropical (Somalia) faunal realms is briefly discussed.

Key words: Oman, Amphibia, Reptilia, zoogeography

Introduction

At present a total of 90 species of reptiles and amphibians are known to occur in the Sultanate of Oman. The largest group are the lizards (including amphisbaenians) with 55 species. The snakes have 28 species, the turtles five species (only marine), and the anurans (toads) two species.

During a field trip to the Sultanate of Oman (fig.1) in November and December 1998 a total of 272 reptiles and amphibians, representing 32 species, were collected. Six additional species were observed but not collected. Most of the material is now kept in the collection of the Museum Koenig, Bonn, Germany (ZFMK). A considerable number of specimen were kept alive to establish breeding colonies in captivity to gain additional information on reproductive biology and behaviour.

The aim of this paper is to provide a preliminary commented list of the material collected during the 1998 expedition to the Sultanate of Oman (followed by a list of localities visited with their respective herpetofaunal communities) and of some material in the ZFMK.

The following literature was used for identification of the material: Arnold 1975, Arnold 1980, Arnold & Gallagher 1975, Leviton et al. 1992 and Salvador 1982.

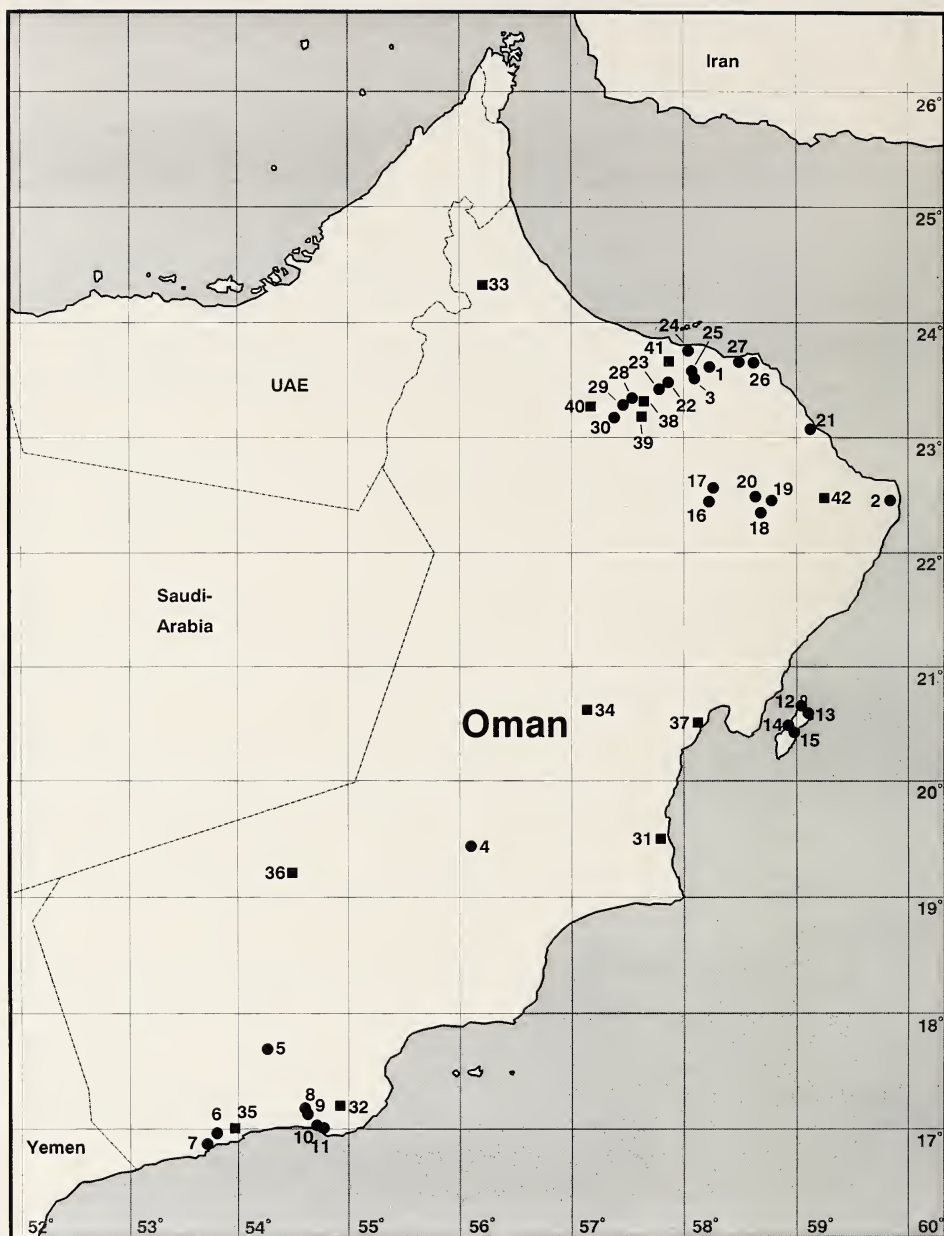


Fig.1: Map of the Sultanate of Oman with collecting sites (circles: collected by Wilms & Hulbert; other material in ZFMK, Bonn.

Commented list

Amphibia

Bufonidae

Bufo arabicus Heyden, 1827

Type locality: "Das petraeische Arabien" (= Sinai Peninsula), Egypt

Localities and collection numbers: ZFMK 71000-003, locality no.17, 28.11.1998; locality no.28, 04.12.1998, still alive; ZFMK 70968-972, locality no.30, 04.12.1998

Distribution: Arabia

We found *Bufo arabicus* in canals used to irrigate the gardens on the edge of an oasis (locality no.17). There we found only adult specimens. The other localities are located in the Wadi bani Awf. In that mesic region tadpoles as well as semiadult and adult specimens were found.

Bufo dhufarensis Parker, 1931

Type locality: Milwah al Aud, Dhofar, Oman

Locality and collection numbers: ZFMK 70973-976, locality no.15, 25.11.1998

Distribution: This species lives in peripheral Arabia from the vicinity of Mecca south to Yemen and eastward to northern Oman.

The toad *Bufo dhufarensis* was found in a Wadi on Masirah Island. According to Meinig & Kessler (1998), spawn and tadpoles were not found in late November and early December. This was confirmed by our observations.

Reptilia

Agamidae

Acanthocercus adramitanus (Anderson, 1896)

Type locality: Hadramaut, Yemen

Locality and collection number: ZFMK 70999, locality no.8, 20.11.1998

Distribution: western and southern Arabia

This specimen was found in Wadi Hinna at the edge of a small clear stream.

Phrynocephalus arabicus Anderson, 1894

Type locality: Plateau of the Hadramaut, Yemen

Localities and collection numbers: ZFMK 41347, locality no.20; ZFMK 66643 & ZFMK 66555-556, locality no.36; ZFMK 70551-552, locality no.37

Distribution: widely distributed in Arabia.

Pseudotrapelus sinaitus (Heyden, 1827)

Type locality: Sinai, Egypt

Localities and collection numbers: ZFMK 70550, locality no.42; sight record, locality no.3, 13.11.1998; ZFMK 70923, locality no.6, 19.11.1998; ZFMK 70998, locality no.9, 20.11.1998; still alive, locality no.10, 20.11.1998

Distribution: Egypt, Sudan, southeastern Libya, Palestine, Jordan, and northern, western and southern parts of Arabia

Uromastix aegyptia microlepis Blanford, 1874

Type locality: vicinity of Basrah, Iraq

Locality: killed by predator, locality no.5, 17.11.1998

Distribution: widespread in Arabia, in the north from Wadi Araba eastwards to western Iran

An old carcass without head was found at the border of a dry Wadi. We did not see any living specimen during the whole trip. Therefore we suppose that this species is hibernating during wintertime.

Uromastix benti (Anderson, 1894)

Type locality: Mukalla, Hadramaut, Yemen

Locality: still alive, locality no.10, 20.11.1998

Distribution: Yemen and southwestern Oman

Uromastix benti was recorded for the first time from the Sultanate of Oman in 1998 (Seufer et al. 1998). We have found this species on the Mirbat plain. The adult specimens inhabit rocky outcrops with a sparse vegetation and retreat into cracks and crevices. The ground was stony. The semiadult specimens were not found in the same area. They inhabited a rocky habitat nearby with a sandy substrate.

Uromastix thomasi Parker, 1930

Type locality: Bu Ju'ay, Rub'al Khali, Oman

Locality and collection number: ZFMK 70413 and alive, locality no.12, 23.11.98-25.11.1998

Distribution: coastal area of southern Oman; Dhofar up to Masirah Island

A dense population of *Uromastix thomasi* was found near Ras Hilf, Masirah Island. The habitat was a stony, in some parts sandy plain with sparse vegetation. The specimens were active from 11.00 to 16.00 h. The temperature of the surface and air temperature one meter above ground was measured. The surface temperature ranged from 37.5 to 51.1°C, while the air temperature was 29.2 - 35.8°C. The body temperature of 24 specimens ranged from 33.1 to 39.4°C. The temperature was measured within 5 minutes of capturing the animal. The temperature in the burrows was between 30.3 and 33.6°C at a depth of 20-41cm. In four burrows temperature at a depth of more than 53 cm was measured. The data are 34°C at 53.5 cm, 31.4°C at 47.5 cm, 29.7°C at 67 cm and 29.6°C at 77.5 cm. The length of the burrows varied between 45 and 165 cm. One specimen played dead after capturing.

Gekkonidae

Asaccus platyrhynchus Arnold & Gardner, 1994

Type locality: Tanuf, Oman

Localities and collection number: sight record, locality no.30, 04.12.1998; ZFMK 70967, locality no.31, 04.12.1998

Distribution: Jebel Akhdar region, northern Oman

One specimen was observed in a small crack together with five *Ptyodactylus hasselquistii* and two *Hemidactylus persicus*. In captivity these animals lay only one single egg per clutch.

Bunopus spatulurus hajarensis Arnold & Gallagher, 1977

Type locality: Wadi Ham, Masafi (25°18.5'N 56°10'E), Oman

Localities and collection numbers: ZFMK 71019, locality no.1, 12.11.1998; ZFMK 71020, locality no.23, 01.12.1998; ZFMK 71018, locality no.25, 01.12.1998

Distribution: eastern UAE, northern Oman south to Masirah island

Bunopus tuberculatus Blanford, 1874

Type locality: Baku Kalat, Bampur and Mand (Baluchistan)

Localities and collection numbers: ZFMK 70888-890, locality no.4, 15.11.1998; still alive, locality no.20, 29.11.1998

Distribution: Palestine, Jordan, southern Iraq, Arabia, Iran, Afghanistan and Pakistan

Cyrtopodion scaber (Heyden, 1827)

Type locality: near Tor, Sinai Peninsula, Egypt

Localities and collection numbers: ZFMK 53524-526, locality no.3; ZFMK 71014-017 and alive, locality no.25, 01.12.1998

Distribution: from Egypt, south to Ethiopia and east to Pakistan

Hemidactylus flaviviridis Rüppell, 1835

Type locality: Massawa, Eritrea

Localities and collection number: ZFMK 53526, locality no.3; sight record, localities 25 and 26, 01.12.1998 and 02.12.1998

Distribution: coastal areas of the Red Sea, Somalia, Arabia; Iraq, Iran, Pakistan, northern India

Hemidactylus homoeolepis Blanford, 1881

Type locality: Socotra, Yemen

Localities and collection numbers: ZFMK 66562, locality no.35; ZFMK 70883, locality no.5, 16.11.1998

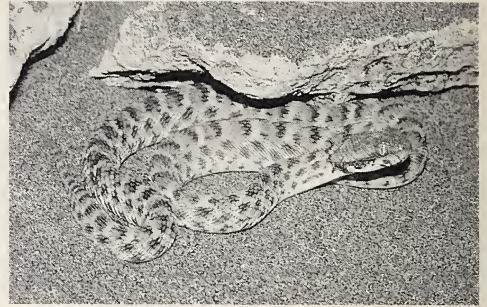
Distribution: Socotra, southern Arabia from Shugra to Ad Daffah near Ras al Hadd (Gardner pers. comm.)

Hemidactylus turcicus parkeri Loveridge, 1936

Type locality: Zanzibar, Tanzania

Locality and collection numbers: ZFMK 70415, ZFMK 70952-953, locality no.13, 23.11.1998

Distribution: coastal areas of the Red Sea, Somalia, southern Arabian littoral as far as eastern UAE, southern Iran, Pakistan



Above left: *Uromastix thomasi* from Masirah Island Photo: Thomas Wilms

Above right: *Echis* cf. *pyramidum* from 3km west of Mirbat Photo: Felix Hulbert

Bottom left: *Pristurus carteri* from 16°58 N, 53°50 E (west of Salalah) Photo: Felix Hulbert

Hemidactylus persicus Anderson, 1872

Type locality: Iran

Locality: still alive, locality no.30, 04.12.1998

Distribution: Iraq, southern Iran, Pakistan, northeastern Saudi Arabia, northern Oman, Bahrain

Hemidactylus yerburii Anderson, 1895

Type locality: Haithalhim and Aden, Yemen

Locality: still alive, locality no.5, 16.11.1998

Distribution: southern Arabia, northern Somalia

Pristurus carteri (Gray, 1863)

Type locality: Masirah Island, Oman

Localities and collection numbers: ZFMK 66554, locality no.36; ZFMK 70899, locality no.2, 12.11.1998; ZFMK 70875-880, ZFMK 70990-992, locality no.5, 16.11.1998; ZFMK 70927-928, locality no.6, 19.11.1998; ZFMK 70983-987, ZFMK 70988-989, locality no.10, 20.11.1998; ZFMK 70934-941, locality no.12, 23.11.1998-26.11.1998; ZFMK 70932-933, locality no.14, 25.11.1998

Distribution: southern Arabia, from northern Yemen to Seeb, northern Oman (Gardner pers. comm.), Masirah island

During the field trip, between 29.11 and 01.12.1998, one female from the vicinity of Thumrait laid one single egg. The juvenile hatched after 70-72 days at 29-30°C.

Pristurus gallagheri Arnold, 1986

Type locality: Rostaq, Jebel Akhdar, northern Oman

Locality: still alive, locality no.30, 04.12.1998

Distribution: Jebel Akhdar

We found *P. gallagheri* on trees and on rocks. The species is arboreal (Gardner 1994).

Pristurus minimus Arnold, 1977

Type locality: Jazir coast, (18° 30'N, 56° 30'E), Oman

Localities and collection numbers: ZFMK 68500, locality no.31; ZFMK 70891-898, locality no.2, 12.11.1998; ZFMK 70942-943, locality no.12, 26.11.1998; sight record, locality no.14, 25.11.1998; ZFMK 70903, locality no.20, 29.11.1998

Distribution: southeastern Arabia

Pristurus rupestris Blanford, 1874

Type locality: Muscat, Oman

Localities and collection numbers: ZFMK 60558, locality no.33; ZFMK 70900-902, locality no.2, 12.11.1998; sight record, locality no.3, 13.11.1998; ZFMK 70885-886, locality no. 5, 16.11.1998; ZFMK 70924-926, locality no.6, 19.11.1998; ZFMK 70994-997, locality no.8, 20.11.1998; sight record, locality no.27, 03.12.1998

Distribution: North-east Africa, Jordan, Arabia and coastal Iran

One hatchling of the Wadi Hinna population measured 12.5 mm (Snout-vent length) and 13 mm (Tail length).

Ptyodactylus hasselquistii (Donndorff, 1798)

Type locality: Cairo, Egypt

Localities and collection numbers: ZFMK 66561, locality no.35; ZFMK 70961-962, locality no.3, 13.11.1998; ZFMK 70881-882, locality no.5, 16.11.1998; ZFMK 70963-966 and alive, localities no.30 & 31, 04.12.1998

Distribution: North-east Africa, Arabia, north to Syria, Iraq and southwestern Iran

At locality no.3 three clutches of *P. hasselquistii* were found in a cave. The diameter of all eggs was 15.8 mm.

Stenodactylus arabicus (Haas, 1957)

Type locality: Abqaiq, near Dharan, Saudi Arabia

Localities and collection numbers: ZFMK 66557-559, locality no.36; ZFMK 66563-564, locality no.34; ZFMK 70979, locality no.18, 28.11.1998

Distribution: Saudi Arabia, UAE, southern Yemen, Oman

ZFMK 70979 was found in sand dunes (Wahiba) with very sparse vegetation at 11.30 h.

Stenodactylus doriae (Blanford, 1874)

Type locality: Bandar Abbas, Iran

Localities and collection numbers: ZFMK 42492, locality no.20; ZFMK 70904-905, ZFMK 70977-978 and alive, locality no.20, 29.11.1998

Distribution: widespread in Arabia, Palestine, Jordan, Iraq, southwestern Iran

Stenodactylus leptocosymbotes Leviton & Anderson, 1967

Type locality: between Dubai and Abu Dhabi (UAE)

Localities and collection numbers: ZFMK 70887, locality no.4, 16.11.1998; ZFMK 70944-950, ZFMK 70414, locality no.12, 24.11.1998; ZFMK 70954-960, locality no.16, 27.11.1998; ZFMK 71004-013, locality no.19, 28.11.1998; ZFMK 70906-922, locality no.20, 29.11.1998

Distribution: southeastern and southern Arabia; eastern UAE and Oman; westwards to southern Yemen

Normally *Stenodactylus leptocosymbotes* prefers harder substrates than *St. doriae* (Arnold 1980). We found both species sympatric in an area with soft sand. Two females from Masirah Island laid two clutches on 31.01.99. The eggs measured 13.7 x 9.7 mm (two eggs), 12.3 x 10 mm and 12.3 x 10.1 mm.

Tropicolotes scorteccii Cherchi & Spanó, 1963

Type locality: El Safa, Yemen

Locality and collection number: ZFMK 66560, locality no.10; still alive, locality no.5, 17.11.1998

Distribution: southern Arabia, Hadramaut and Dhofar

Lacertidae

Acanthodactylus blanfordii Boulenger, 1918

Type locality: "Perse et Béloutchistan"

Locality: still alive, locality no.24, 01.12.1998

Distribution: southeastern Iran, western Pakistan, southern Afghanistan and northern coast of the Sultanate of Oman

Acanthodactylus boskianus (Daudin, 1802)

Type locality: Egypt

Locality: sight record, locality no.17, 28.11.1998

Distribution: North Africa, Arabia northwards to the Turkish border

Acanthodactylus felcis Arnold, 1980

Type locality: Hadramaut, southern Yemen

Locality and collection number: ZFMK 70981, locality no.10, 20.11.1998

Distribution: southern Yemen and Dhofar

The only character given by Arnold (1986) to distinguish *A. felcis* from *A. yemenicus* is the number of ventral scales across the belly (usually 8 in *felcis* and usually 10 in *yemenicus*). The specimen in question has 8 scales in longest row across the belly.

Acanthodactylus felcis occupies sandy substrates (Arnold 1980). We found this species on a harder substrate in association with *Uromastix benti*, *Pseudotrapelus sinaitus*, *Pristurus carteri*, *Mabuya* spec. and *Echis* cf. *pyramidum*.

Acanthodactylus schmidtii Haas, 1957

Type locality: Dharan, Saudi Arabia

Locality and collection number: ZFMK 70980, locality no.20, 30.11.1998

Distribution: Arabia north to Jordan; absent from the western and southwestern parts of Arabia and from the Batina (Oman)

Mesalina adramitana (Boulenger, 1917)

Type locality: Hadhramaut, Yemen

Localities and collection numbers: ZFMK 70884, locality no.5, 17.11.1998; ZFMK 70951, locality no.12, 26.11.1998

Distribution: southern and southeastern Arabia

Mesalina cf. ayunensis Arnold, 1980

Type locality: Ayun, Dhofar, Oman

Locality and collection number: ZFMK 66566, locality no.32

Distribution: Dhofar, Sultanate of Oman

Omanosaura cyanura (Arnold, 1972)

Type locality: Wadi Shawkah (25°06'N 56°03'E), Trucial States (= United Arab Emirates)

Localities and collection numbers: ZFMK 56397, locality no.38; ZFMK 56398, locality no.39

Distribution: northern Oman (Musandam, Jebel Akhdar), eastern UAE

Omanosaura jayakari (Boulenger, 1887)

Type locality: Muscat, Oman

Localities and collection numbers: ZFMK 63696-697, locality no.40; sight record, locality no.29, 04.12.1998

Distribution: northern Oman and UAE

Scincidae

Chalcides ocellatus (Forskål, 1775)

Type locality: Egypt

Locality: sight record, locality no.11, 21.11.1998

Distribution: North Africa, coastal area of Arabia, South-west Asia to Pakistan

Mabuya spec.

Locality: sight record, locality no.10, 20.11.1998

Scincus mitranus Anderson, 1871

Type locality: Arabia

Localities: sight record, locality no.5, 17.11.1998; still alive, locality no.18, 28.11.1998

Distribution: Arabia with exception of the western and northwestern parts

Colubridae

Coluber rhodorachis (Jan, 1865)

Type locality: Persia

Localities and collection numbers: ZFMK 70930, locality no.7, 19.11.1998; ZFMK 70929, locality no.21, 30.11.1998; sight records, localities no.29 & 30, 04.12.1998

Distribution: North-east Africa to northern India, western and southern Arabia

Lytorhynchus diadema (Duméril, Bibron & Duméril, 1854)

Type locality: Algeria

Locality and collection number: ZFMK 70931, locality no.41

Distribution: North Africa and Arabia

Viperidae

Echis carinatus sochureki Stemmler, 1969

Type locality: Ban-Kushdil-Khan, Pishin, Pakistan

Locality: still alive, locality no.1, 12.11.1998

Distribution: Arabia, the UAE and northern Oman

Echis coloratus Günther, 1878

Type locality: Jebel Sharr [country?]

Locality: still alive, locality no.5, 16.11.1998

Distribution: Egypt, Sinai, Israel, Jordan, western rocky mountain areas of Arabia, south to the Hadramaut; northern and central Oman

Echis cf. *pyramidum* (Geoffroy St. Hilaire, 1827)

Type locality: Egypt

Locality: still alive, locality no.10, 20.11.1998

Distribution: southwestern Arabia, Yemen and Oman

Zoogeographical discussion

Because of its position at the border between the Afrotropical and Palearctic biogeographic regions, southern Arabia is of particular interest. Arabia is mainly classified as part of the Saharo-Sindian Subregion of the Palearctic Region. Only the southwest (Yemen and southern Oman) is part of the Afrotropical subregion of the Palearctic region.

Arabia is separated from Somalia in eastern Africa only by the Gulf of Aden. Despite the narrowness of the water barrier between Arabia and the African mainland it marks a very abrupt faunal change. This is especially surprising because of the supposed land connection between Arabia and Somalia during the Pleistocene eustatic sea level changes (Arnold 1987, Joger 1987, Lanza 1988). For example, only 25 reptilian species of approximately 197 non-marine species in Somalia can be found in Arabia, of which only 14 species inhabit the Sultanate of Oman (*Bitis arietans*, *Chalcides ocellatus*, *Coluber rhodorachis*, *Echis* cf. *pyramidum*, *Hemidactylus yerburii*, *H. turcicus parkeri*, *Leptotyphlops macrorhynchus*, *Mabuya brevicollis*, *Naja haje*, *Pristurus rupestris*, *Ptyodactylus hasselquistii*, *Psammophis schokari*, *Ramphotyphlops braminus* and *Telescopus dhara*). Of the 29 amphibian species of Somalia, none is known to occur in Oman. Besides the above mentioned genera, Somalia and Oman share species of the genera *Atractaspis*, *Acanthocercus*, *Bufo*, *Chamaeleo*, *Eryx*, *Mesalina*, *Spalerosophis*, *Tropicolotes*, *Uromastix* and *Varanus*. Of those, *Acanthocercus*, *Atractaspis*, *Bitis*, *Chamaeleo* and *Mabuya* are of Afrotropical origin.

Table 1: List of localities

no.	GPS-data	Location	Species
1	23° 37 N 58° 10 E	Vicinity of Seeb Airport	<i>Echis carinatus sochureki</i> , <i>Bunopus spatulurus hajarensis</i>
2	22° 25 N 59° 49 E	Ras al Hadd sea-turtle protecto- rate	<i>Pristurus minimus</i> , <i>P. rupestris</i> , <i>P. car- teri</i>
3	23° 34 N 58° 08 E	Vicinity of Al-Khoud / Univer- sity	<i>Ptyodactylus hasselquistii</i> , <i>Pristurus rupestris</i> , <i>Pseudotrapelus sinaitus</i>
3	–	Al-Khoud	<i>Hemidactylus flaviviridis</i> , <i>Cyrtopodion scaber</i>
4	19° 27 N 56° 04' E	67 km from Haima in direction of Marmul	<i>Bunopus tuberculatus</i> , <i>Stenodactylus leptocosymbotes</i>
5	17° 40 N 54° 09 E	27 km fromThumrait in direction of Marmul	<i>Echis coloratus</i> , <i>Ptyodactylus hassel- quistii</i> , <i>Hemidactylus homoeolepis</i> , <i>H. yerburyii</i> , <i>Pristurus rupestris</i> , <i>P. carte- ri</i> , <i>Mesalina adramitana</i> , <i>Uromastyx aegyptia microlepis</i> , <i>Tropiocolotes scoretcei</i> , <i>Scincus mitranus</i>
6	16° 58 N 53° 50 E	West of Salalah	<i>Pristurus rupestris</i> , <i>P. carteri</i> , <i>Pseudo- trapelus sinaitus</i>
7	–	4 km before Mughsayl	<i>Coluber rhodorachis</i>
8	–	Wadi Hinna, pool below the re- sting place	<i>Acanthocercus adramitanus</i> , <i>Pristurus rupestris</i>
9	–	1 km from Wadi Hinna in directi- on of Mirbat	<i>Pseudotrapelus sinaitus</i>
10	17°00 N 54°42'E	3 km west of Mirbat	<i>Uromastyx benti</i> , <i>Acanthodactylus feli- cis</i> , <i>Mabuya spec.</i> , <i>Echis cf. pyrami- dum</i> , <i>Pseudotrapelus sinaitus</i> , <i>Pristurus carteri</i>
10	–	near Mirbat	<i>Tropiocolotes scoretcei</i>
11	–	City of Mirbat	<i>Chalcides ocellatus</i>
12	–	Northern Masirah	<i>Uromastyx thomasi</i>
12	–	<i>thomasi</i> - habitat	<i>Pristurus carteri</i> , <i>P. minimus</i> , <i>Steno- dactylus leptocosymbotes</i> , <i>Mesalina adramitana</i>
13	–	Masirah Hotel	<i>Hemidactylus turcicus parkeri</i>
14	20° 22 N 58° 47 E	Central Masirah	<i>Pristurus carteri</i> , <i>P. minimus</i>
15	20° 30 N 58° 54 E	Wadi Blad Central Masirah	<i>Bufo dhufarensis</i>
16	22° 25 N 58° 11 E	3 km before Sanaw	<i>Stenodactylus leptocosymbotes</i>
17	22° 33 N 58° 11 E	Al Bolydah	<i>Bufo arabicus</i> , <i>Acanthodactylus boskia- nus</i>
18	22° 23 N 58° 45 E	Wahiba Sands	<i>Scincus mitranus</i> , <i>Stenodactylus arabi- cus</i>
19	22° 28 N 58° 47 E	2 km from A`Shariq in direction of Muscat,	<i>Stenodactylus leptocosymbotes</i>
20	22° 30 N 58° 39 E	Wahiba Sands	<i>Stenodactylus doriae</i> , <i>S. leptocosymbo- tes</i> , <i>Bunopus tuberculatus</i> , <i>Acantho- dactylus schmidtii</i> , <i>Pristurus minimus</i>
20	–	approximately 100 km inland of Muscat	<i>Phrynocephalus arabicus</i> , <i>Stenodacty- lus doriae</i>

21	23° 08 N 58° 07 E	Sur – Muscat 106 km to Muscat	<i>Coluber rhodorachis</i>
22	23° 32 N 57° 51 E	Barka, in direction of Al Rustaq	<i>Echis carinatus sochureki</i>
23	23° 29 N 57° 50 E	6 km NE of Afi	<i>Bunopus spatulurus hajarensis</i>
24	23° 42 N 58° 02 E	dunes behind Al-Naseem park	<i>Acanthodactylus blanfordi</i>
25	–	Sultan Qaboos University Campus	<i>Cyrtopodion scaber</i> , <i>Bunopus spatulurus hajarensis</i> , <i>Hemidactylus flaviviridis</i>
26	–	Muscat	<i>Hemidactylus flaviviridis</i>
27	–	National Museum of Natural History - Botanical Garden	<i>Pristurus rupestris</i>
28	23° 17 N 57° 28 E	Wadi Bani Awf 2-3 km SW of Far	<i>Bufo arabicus</i>
29	–	10 km from no. 28	<i>Omanosaura jayakari</i> , <i>Coluber rhodorachis</i>
30	23° 12 N 57° 23 E	Wadi Bani Awf near Bimah	<i>Ptyodactylus hasselquistii</i> , <i>Hemidactylus persicus</i> , <i>Asaccus platyrhynchus</i> , <i>Bufo arabicus</i> , <i>Coluber rhodorachis</i> , <i>Pristurus gallagheri</i>
30	23° 14 N 57° 26 E	Wadi Bani Awf	<i>Asaccus platyrhynchus</i> , <i>Ptyodactylus hasselquistii</i> , <i>Hemidactylus persicus</i> , <i>Bufo arabicus</i>
31	–	Dhofar between Duqm and Surayr	<i>Pristurus minimus</i>
32	–	Dhofar/ Jebel Samhan	<i>Mesalina cf. ayunensis</i>
33	–	Khutwa	<i>Pristurus rupestris</i>
34	–	Umm az Zumaim	<i>Stenodactylus arabicus</i>
35	–	Wadi Raysut	<i>Ptyodactylus hasselquistii</i> , <i>Hemidactylus homoeolepis</i>
36	–	Quit Bit	<i>Pristurus carteri</i> , <i>Phrynocephalus arabicus</i> , <i>Stenodactylus arabicus</i>
37	–	Near Khaluf / Wahiba Sands	<i>Phrynocephalus arabicus</i>
38	–	Wadi near Al Ghubrah	<i>Omanosaura cyanura</i>
39	–	Wadi near Al Hammah	<i>Omanosaura cyanura</i>
40	–	Near Manda	<i>Omanosaura jayakari</i>
41	–	between Barka and Al Rustaq	<i>Lytorhynchus diadema</i>
42	–	Wadi Bani Khalid / Wahiba Sands	<i>Pseudotrapelus sinaitus</i>

In the east, southern Arabia is separated from Iran by the Gulf of Oman and the Arabian Gulf. Of approximately 168 taxa of non-marine reptiles found in Iran (Anderson 1974, Latifi 1991), 24 taxa also occur in Oman: *Acanthodactylus blanfordii*, *Acanthodactylus schmidtii*, *Ablepharus pannonicus*, *Bunopus tuberculatus*, *Chalcides ocellatus*, *Calotes versicolor* (presumably introduced), *Coluber rhodorachis*, *Diplometopon zarudnyi*, *Echis carinatus sochureki*, *Eryx jayakari*, *Hemidactylus flaviviridis*, *Hemidactylus persicus*, *Leptotyphlops macrorhynchus*, *Mabuya aurata*, *Malpolon moilensis*, *Phrynocephalus maculatus*, *Pristurus rupestris*, *Ptyodactylus hasselquistii*, *Psammophis schokari*,

Pseudocerastes persicus, *Spalerosophis diadema*, *Stenodactylus doriae*, *Uromastix aegyptia microlepis* and *Varanus griseus*.

In addition, on a generic level Oman and Iran share species of the genera *Asaccus*, *Lytorhynchus*, *Tropicolotes*, *Mesalina* and *Scincus*. In general, northern Oman has strong affinities with Iran and southern Pakistan (Baluchistan) while southern Oman (Dhofar) has affinities with the Horn of Africa.

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Zusammenfassung

Zur Herpetofauna des Sultanats von Oman, mit Hinweisen zur Beziehung zwischen afrotropischer und saharosindischer Fauna

Heute sind insgesamt 90 Arten von Amphibien und Reptilien aus dem Gebiet des Sultanats von Oman bekannt. Während einer Forschungsreise in das Sultanat konnten 272 Exemplare von Reptilien und Amphibien aus 32 Arten gesammelt werden. Sechs weitere Arten wurden nachgewiesen aber nicht gesammelt. Weiteres Material aus der Sammlung des ZFMK wurde einbezogen, so daß insgesamt 42 Arten von Amphibien und Reptilien in einer kommentierten Liste aufgeführt sind; es folgt eine Liste der besuchten Lokalitäten mit ihren entsprechenden Herpetozöosen. Die Beziehungen der omanischen Herpetofauna zur paläarktischen Herpetofauna des Irans und der afrotropischen Herpetofauna Somalias werden aufgezeigt.

References

- Anderson, S. (1974): Preliminary Key to the Turtles, Lizards and Amphisbaenians of Iran. – *Fieldiana Zoology* 65(4): 27-44.
- Arnold, E. (1975): Little-known Geckoes (Reptilia: Gekkonidae) from Arabia with description of two new species from the Sultanate of Oman. – *J. Oman Stud. Spec. Rep.* 1: 81-110.
- Arnold, E. (1980): The Reptiles and Amphibians of Dhofar, Southern Arabia. – *J. Oman Stud. Spec. Rep.* 2: 273-332.
- Arnold, E. (1986): A Key and Annotated Check List to the Lizards and Amphisbaenians of Arabia. – *Fauna of Saudi Arabia* 8: 385-435.
- Arnold, E. (1987): Zoogeography of the Reptiles and Amphibians of Arabia. – *Proc. Symp. Fauna Zoogeogr. Middle East*: 246-256.

- Arnold, E. & M. Gallagher (1975): Reptiles and Amphibians from the Mountains of Northern Oman. – J. Oman Stud. Spec. Rep. 1: 59-80.
- Gardner, A. S. (1994): *Pristurus gallagheri*, an arboreal semaphore gecko from Oman, with notes on its tail flagging behaviour. – Dactylus 2: 126-129.
- Joger, U. (1987): An Interpretation of Reptile Zoogeography in Arabia, with Special Reference to Arabian Herpetofaunal Relations with Africa. – Proc. Symp. Fauna Zoogeogr. Middle East: 257-271.
- Lanza, B. (1988): Amphibians and reptiles of the Somali Democratic Republic: check list and biogeography. – Biogeographia 14: 407-465.
- Latifi, M. (1991): The snakes of Iran. – Society for the Study of Amphibians and Reptiles 159 pp.
- Leviton, A., S. Anderson, K. Adler & A. Minton (1992): Handbook to Middle East Amphibians and Reptiles. – Society for the Study of Amphibians and Reptiles 252 pp.
- Meinig, H. & H. Kessler (1998): Herpetologische Beobachtungen im Rahmen einer Nationalparksplanung: Barr al Hikman und Masirah Island, Sultanat von Oman (Amphibia; Reptilia). – Faun. Abh. 21 (Suppl.): 89-97.
- Salvador, A. (1982): A Revision of the Lizards of the Genus *Acanthodactylus* (Sauria: Lacertidae). – Bonn. zool. Monogr. 16, 167 pp.
- Seufer, H., T. Kowalski, U. Prokoph & H. Zilger (1998): Erstnachweis von *Uromastix benti* (Anderson, 1894) für den Oman (Provinz Dhofar). – Herpetofauna 20(114): 22-23.

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The evolution of *Microtia* Freudenthal, 1976 (Mammalia, Rodentia), an endemic genus from the neogene of the Gargano island, southern Italy

Virginie Millien-Parra

Abstract: The Gargano area, considered as a Late Neogene paleoisland, has yielded many micromammal remains from numerous karstic fissures. All described species show extraordinary morphological peculiarities, due to island evolution.

Among the seven murid rodent genera recognized, *Microtia* is the most abundant and is represented by three main lineages that differ in size. These three lineages were evidenced through a study of molar size and morphology, the size evolution of the first lower molar being the basis for a biostratigraphic time scale of the Gargano fissures.

Isolated endemic rodents often evolve towards gigantism, but many recent studies have pointed out the role of interspecific competitive interactions on community size structure, which can also greatly influence species size evolution. The occurrence of numerous karstic localities of different ages in the Gargano paleoisland, and the abundance of *Microtia* in each of these localities, provided a unique opportunity to investigate size structure of the *Microtia* community and its evolution.

Microtia body size was inferred from the lower incisor size which is known to be highly correlated to body size among extant rodent species. The three lineages did not follow the same evolutionary size trend: two of them evolved towards gigantism, while the third tended towards a smaller size. In addition, I characterized the evolution of the lower incisor curvature and concluded that *Microtia* was characterized by a specialization for burrowing which was accompanied by both an increase or a decrease in size. Finally, the evolutionary size changes among the three sympatric *Microtia* lineages allowed the minimization of competition between them.

Key words: isolated rodent, incisor, Gargano, Neogene, size evolution

Introduction

The Gargano fossil localities and their mammalian fauna

The Gargano peninsula is located in southern Italy, in Foggia province. In addition to the geological evidence, the highly differentiated and impoverished fauna of the Gargano clearly indicates that the Gargano is a paleoisland that remained isolated during several million years (fig.1). The Gargano vertebrate remains were discovered by M. Freudenthal, in the early 1970s, where the fossils were found in numerous karstic localities (fig.2) that span an imprecise time interval between the Late Miocene and the Early Pliocene (Freudenthal 1976, Abbazzi et al. 1996).

The Gargano mammalian fauna is impoverished, with only some representatives of four orders: the insectivores, rodents, lagomorphs, and artiodactyls. Carnivores, perissodactyls and proboscidiens are missing. Most of the taxa described to date show extraordinary morphological peculiarities, and, in general, a remarkable tendency towards the gigantism that has been associated with island evolution

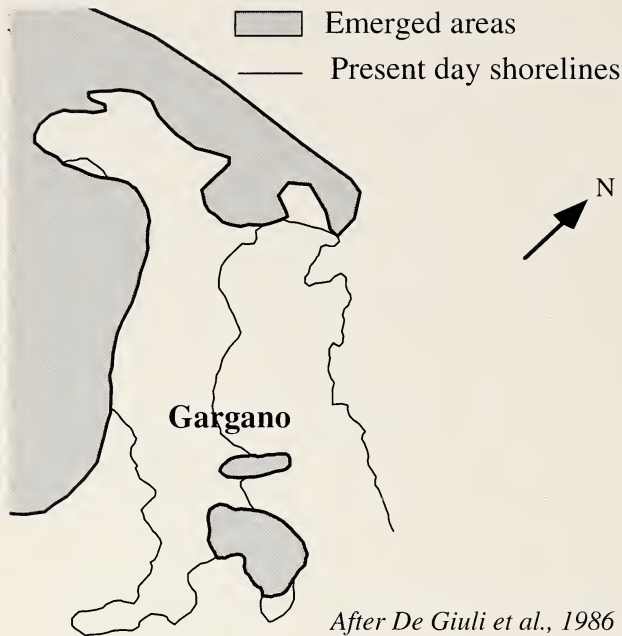


Fig.1: Paleogeographic reconstruction of the Gargano area during the late Neogene. The Gargano peninsula is a paleoisland that remained isolated during several million years. (modified, after De Giuli et al. 1986).

(Freudenthal 1972, Ballmann 1973, 1976, Willemsen 1983, Leinders 1984). The Gargano fauna all became extinct after the establishment of a connection of the area to the Italian mainland in the early Pleistocene.

Within these endemic forms, two taxa of mammals show tremendous morphological specializations. The first one, *Deinogalerix*, is a giant insectivore, but due to its large size it probably included small mammals in its diet, and was thus probably closer to a scavenger in its habit (Freudenthal 1972). This taxon is probably the largest insectivore ever found, with a skull of approximately 20 cm in length. The second taxon, *Hoplitomeryx*, belongs to the Ruminantia and was so differentiated that it is considered as a family-level endemic to the Miocene of southern Italy (Leinders 1984). The five horns on the skull in this taxon is a very good example of great morphological innovation.

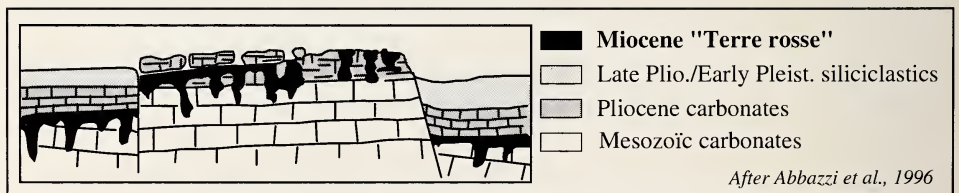


Fig.2: The Gargano fossils were discovered in numerous karstic fissures that span an imprecise time interval between the late Miocene and the early Pliocene (modified, after Abbazzi et al. 1996).

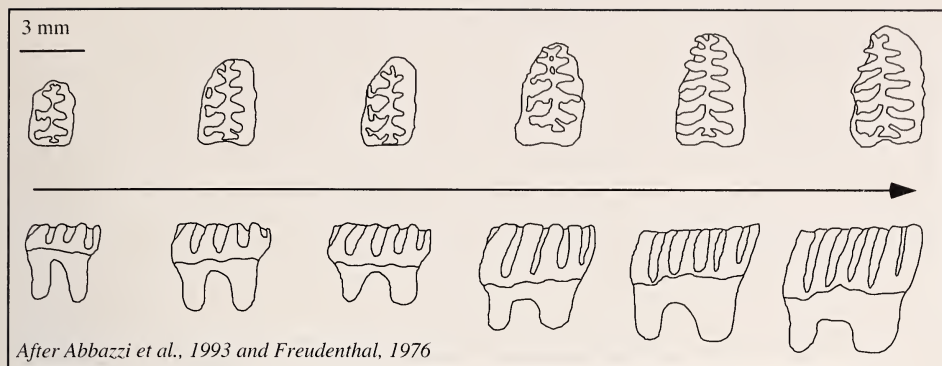


Fig.3: The evolution of the M/1 from *Microtia*. This evolution is characterized by an increase in size and by the development of additional lamellae at the anterior end of the M/1. (modified, from Freudenthal 1976 and Abbazzi et al. 1993).

Another very peculiar taxon from the Gargano fauna is the rodent genus *Microtia*, which is the most abundant rodent among the seven rodent species described to date, and is represented by three main lineages that differ in size. *Microtia* molars have been previously described (fig.3), and the evolution of the main middle-sized lineage is the basis for a biostratigraphic time scale of the Gargano fissures (Abbazzi et al. 1993, Freudenthal 1976). The evolution of this lineage is characterized by an increase in molar size and by the development of additional lamellae at the anterior end of the first lower molar, M/1, and at the back of the third upper molar, M3/ (Freudenthal 1976). In a recent study of the *Microtia* skull (Parra et al. 1999), we proposed that some of its morphological characteristics indicated an adaptation for a burrowing life, which is unique for a murine rodent. Some of these characteristics are, for example, an elongated snout, highly proodont upper and lower incisors, and the presence of a huge bony apophysis on the squamosal bone for the insertion of the temporal muscle (fig.4).

Here, I propose to review the morphological and size evolution of the lower incisor of this very peculiar rodent genus.

The information yielded from incisors

Rodent species are characterized by one upper and lower incisor pair with continuous growth that display a great variation in size, shape and morphology. However, the information contained in these incisors is usually not considered in paleontological studies. The main reason for using incisors is that microfossil layers contain numerous incisors, isolated, or still connected to the upper or lower jaws.

Secondly, both upper and lower incisors are accurate estimators of body weight among rodents (Parra & Jaeger 1998). The following equation describes the relationship between the antero-posterior diameter of the lower incisor (AP, in mm) and body weight (W, in g) for species of extant rodents:

$$\log W = (2.58 * \log AP) + 3.18 \text{ [Eq. 1]}$$

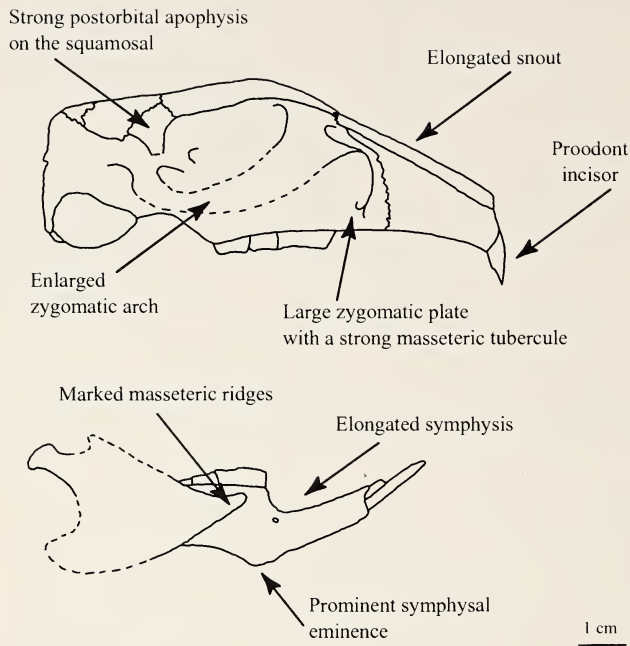


Fig.4: The skull of *Microtia*, in lateral view. An elongated snout, highly proodont upper and lower incisors and the presence of a huge bony apophysis on the squamosal are some of its morphological characteristics (modified, from Parra *et al.* in press).

This relation is highly significant ($r = 0.93$, $p < 0.001$), and, applying the hypothesis that it has not changed through time, we can apply it to fossil rodent species.

The evolution of rodent species on islands

The general pattern of insular evolution amongst mammals indicates that small species become larger on islands, and large species become smaller (Foster 1964, van Valen 1973). Several hypotheses have been proposed to explain the increase in the size of isolated rodent species. The most important ones are:

- (1) Resource limitation on islands favors K-strategies among rodents, and consequently an increase in their body size;
- (2) Decreased predation (Heaney 1978), or the absence of predators on islands (Valverde 1964) allows rodent species to reach a larger size. Under predation pressure on the mainland rodent species stay small in order to escape from predators;
- (3) The existence of a physiological optimal body size that can be reached by isolated mammals (Brown *et al.* 1993, Damuth 1993);
- (4) Finally, the decreased number of competing species on islands allows isolated species to increase their range of exploitable resources, and consequently their body size (Lomolino 1985).

I will test each of these hypotheses using the *Microtia* assemblage and its evolution. In addition, I will indicate adaptive changes in behaviour for *Microtia*.

The case of *Microtia*

The evolution of size

The hypothesis of resource limitation is difficult to assess in the case of the Gargano fauna, because of insufficient data on the paleoenvironment of this area.

Fig.5 provides a schematic representation of the evolution of the three *Microtia* lineages. It is based on almost 400 specimens that were collected in 11 different fissures. Complete data measurements are given elsewhere (Parra & Jaeger, manuscript). The size character used is the antero-posterior diameter of the lower incisor, which is used as a body size estimator (Eq. 1). The first observation is that the evolutionary size trends are different for the three lineages: the two largest lineages evolving towards larger size, the smallest one tending towards smaller size. The evolution towards a larger size is in accordance with the general observations made on other isolated rodents (Foster 1964, Sondaar 1977, Case 1978, Heaney 1978, Lawlor 1982, Adler & Levins 1994), but it is difficult to explain the size trend observed for the smallest lineage.

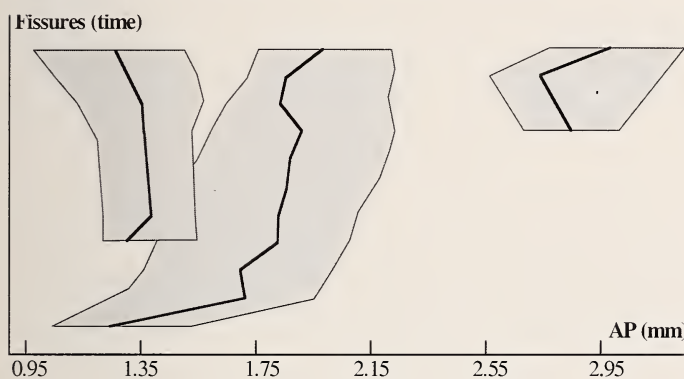


Fig.5: Schematic representation of the evolutionary size trends observed for the three *Microtia* lineages, based on the lower incisor size (modified from Parra & Jaeger, manuscript). Grey areas represent the total range and lines indicate the mean values of the lower incisor size (antero-posterior diameter, AP, in mm).

Two approaches have led to the hypothesis of an existence of an optimal body size among mammalian species. The first one was based on the relation between body mass and population density among mammals (Damuth 1993). Here it is proposed that there is an optimal body size for intermediate body size species, around 1 kg, these species being more efficient at energy acquisition.

The second approach was described by Brown et al. (1993). The species' body size is affected by both the rate of acquisition of environmental resources and the rate of conversion of these resources for reproduction. This last model predicts that there is an optimal body size for small body species of around 100 g.

In these two studies it is claimed that the theory of an optimal body size provides an explanation for the island-rule, i.e. evolution towards a larger size of small mammals and a smaller size of large species (Brown et al. 1993, Damuth 1993). However, the two values proposed are very different – a difference of an order of magnitude. The available data on isolated rodent species do not favour either one of these hypotheses. However, a tabulation of all known isolated species body sizes may be helpful for further clarification of this point. Importantly, the results

obtained for *Microtia* do not provide any evidence for the existence of an optimal body size, because of the different directions of evolutionary size trends observed for each *Microtia* lineage.

The hypothesis of reduced predation does not find support here, because many potential predators for *Microtia* were discovered in the Gargano fossil remains. One of these predators is the giant insectivore, *Deinogalerix*, which probably included small mammals in its diet (Freudenthal 1972). But the most interesting one is a giant owl that was likely to have preyed heavily on *Microtia*. This owl genus, *Tyto*, like *Microtia*, is also represented by three lineages that differ in size (Ballmann 1976). The most interesting observation that can be made concerning the size evolution of the two genera *Microtia* and *Tyto* is that their evolutionary size trends are very similar, the two largest lineages evolving towards a larger size while the smallest lineage tends towards a smaller size. This could suggest predator/prey coevolution, or, at least, that owl size was tracking rodent size.

The last hypothesis proposed was reduced competition between species on islands. In the case of *Microtia*, however, I am led to suggest that competition between the different species was still strong. Indeed we can observe an increase in the size differences between species through time, which can be explained by the existence of competition between them. Interspecific competition is therefore the only hypothesis that can explain the different size trends observed for the *Microtia* lineages.

Changes in behaviour

The evolution of the shape of the incisor can be indicative of some adaptive changes in *Microtia*. As a first approximation, I used the radius of incisor curvature to characterize the lower incisor shape. The evolutionary patterns observed for the lower incisor size and shape of *Microtia* are always characterized by an increase in the radius of incisor curvature, which can be accompanied by an increase or a decrease in size. Procumbent incisors are one of the morphological characteristics of burrowing rodents (Dubost 1968, Gasc et al. 1985, Lessa 1990). Hence this result can be interpreted as an improvement of the burrowing adaptation, whether with an evolution towards nanism or gigantism.

The evolution of body weight

In addition, I used the relationship established for extant rodent species between the size of the lower incisor and body weight (Eq. 1). Body weight was estimated for the main middle-sized lineage at its oldest and youngest fissures of occurrence. If *Microtia* weighed a little more than 40 g in the oldest fissure, there is a huge increase in weight through time, since it reaches more than 140 g in the youngest fissure, an increase of more than 230%. Such an increase in weight implies great changes in physiology accompanying the increase in size. Such a large increase in body weight might be related, for example, to a reduction in reproductive output, population density and energetic expenditure per unit weight (Peters 1983, Adler & Levins 1994), all of which would enhance the probability of extinction of the *Microtia* fauna on reconnection with the mainland in the early Pleistocene.

Conclusion

We proposed that the evolutionary size patterns observed for *Microtia* were mainly the result of competition between species, which is in accordance with previous results from some mainland rodent communities (Dayan et al. 1994, Parra et al., 1999). However, other factors, such as predation pressure or evolution towards an optimal body size, do not appear to be important in the particular case of *Microtia*.

In conclusion, the evolution in the rodent genus *Microtia* brought about changes not just in size but, with the improvement of the adaptation to a burrowing life, also in behaviour. The large increase in body weight, concurrent with body size change, was also likely to have led to substantial changes in physiology.

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References

- Abbazzi, L., F. Masini & D. Torre (1993): Evolutionary patterns in the first lower molar of the endemic murid *Microtia*. – Quaternary Int. 19: 63-70.
- Abbazzi, L., M. Benvenuti, G. Boschian, S. Dominici, F. Masini, C. Mezzabotta, L. Piccini, L. Rook, G. Valleri & D. Torre (1996): Revision of the Neogene and Pleistocene of the Gargano region (Apulia, Italy). The marine and continental successions and the mammal faunal assemblages in an area between Apricena and Poggio Imperiale (Foggia). – Memorie della Società Geologica Italiana 51: 383-402.
- Adler, G.H., & R. Levins (1994): The Island Syndrome in Rodent Populations. – Quatern. rev. Biol. 69: 473-490.
- Ballmann, P. (1973): Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien). – Scripta Geol. 17: 1-75.
- Ballmann, P. (1976): Fossile Vögel aus dem Neogen der Halbinsel Gargano (Italien), 2. Teil. – Scripta Geol. 38: 1-59.
- Brown, J.H., P.A. Marquet & M.L. Taper (1993): Evolution of Body Size: Consequences of an energetic definition of fitness. – Amer. Nat. 142: 573-584.
- Case, T.J. (1978): A general explanation for insular body size trends in terrestrial vertebrates. – Ecology 59: 1-18.
- Damuth, J. (1993): Cope's rule, the island rule and the scaling of mammalian population density. – Nature 365: 748-750.

- Dayan, T., & D. Simberloff (1994): Morphological relationships among coexisting heteromyids: an incisive dental character. – *Amer. Nat.* 143: 462-477.
- Dubost, G. (1968): Les mammifères souterrains. – *Rev. Ecol. Biol. Sol* V: 99-133.
- De Giuli, C., F. Masini & D. Torre (1986): Endemism and bio-chronological reconstructions: the Gargano case history. – *Boll. Soc. Paleontol. Ital.* 25: 267-276.
- Foster, J.B. (1964): Evolution of mammals on islands. – *Nature* 202: 234-235.
- Freudenthal, M. (1972): *Deinogalerix koenigswaldi* nov. gen., nov. spec., a giant insectivore from the Neogene of Italy. – *Scripta Geol.* 14: 1-11.
- Freudenthal, M. (1976): Rodent stratigraphy of some Miocene fissure fillings in Gargano (prov. Foggia, Italy). – *Scripta Geol.* 37: 1-20.
- Gasc, J.-P., S. Renous, A. Casinos, E. Laville & J. Bou (1985): Comparison of diverse digging patterns in some small mammals. – pp. 35-38 in: *Vertebrate Morphology* (eds: Duncker, H.-R. & G. Fleischer). – Gustav Fisher Verlag, Stuttgart, New York.
- Heaney, L.R. (1978): Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of southeast Asia. – *Evolution* 32: 29-44.
- Lawlor, T.E. (1982): The evolution of body size in mammals: evidence from insular populations in Mexico. – *Amer. Nat.* 119: 54-72.
- Leinders, J. (1984): *Hoplitomerycidae* fam. nov. (Ruminantia, Mammalia) from Neogene fissure fillings in Gargano, Italy. Part 1. – *Scripta Geol.* 70: 1-51.
- Lessa, E.P. (1990): Morphological Evolution of Subterranean Mammals: Integrating Structural, Functional, and Ecological Perspectives. – pp. 211-230 in: *Evolution of Subterranean Mammals at the Organismal and Molecular level* (eds. Nevo, E. & O.A. Reig). – Wiley-Liss, New-York.
- Lomolino, M.V. (1985): Body size of mammals on islands: the island rule reexamined. – *Amer. Nat.* 125: 310-316.
- Parra, V. & J.-J. Jaeger (1998): Estimation de la taille et du poids corporel chez les rongeurs (Rodentia, Mammalia) à partir de la taille des incisives. – *C. R. Acad. Scien., Série Ila, Scien. Terre Planètes* 326: 79-85.
- Parra, V., M. Loreau & J.-J. Jaeger (1999): Incisor size and community structure in rodents: Two tests of the role of competition. – *Acta Oecol.* 20: 93-101.
- Parra, V., J.-J. Jaeger & H. Bocherens (in press): The skull of *Microtia* (Freudenthal, 1976), an extinct burrowing murine rodent genus of the late Neogene of Gargano, South Italy. – *Lethaia*.
- Peters, R.H. (1983): The ecological implications of body size. – Cambridge University Press, London.
- Sondaar, P. Y. (1977): Insularity and its effect on mammal evolution. – pp. 671-705 in: *Major Patterns in vertebrate Evolution* (eds. Hecht, M.K. & P.C. Goody). – Plenum Press, New-York, London.

- Valverde, J.A. (1964): Remarques sur la structure et l'évolution des communautés de vertébrés terrestres I. Structure d'une communauté II. Rapports entre prédateurs et proies. – *Terre et la Vie* 2: 121-154.
- van Valen, L.M. (1973): A new evolutionary law. – *Evolutionary Theory* 1: 1-30.
- Willemsen, G.F. (1983): *Paralutra garganensis* sp. nov. (Mustelidae, Lutrinae), a new otter from the Miocene of Gargano, Italy. – *Scripta Geol.* 72: 1-8.

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ABSTRACTS

Arboreal Squamates in Tropical Forests of Vietnam: Species Richness, Natural History and Conservation

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Herpetofauna of the tropical montane forests in Tonkin and Annam includes about 90 species of lizards and 140 species of snakes. For squamate assemblages of tropical forests a considerable percentage of arboreal forms is typical. In the fauna of Vietnam about 50 lizard species and 70 snake species demonstrate the adaptations to the arboreal mode of life developed to different extent. It is well known that the spatial structure of the herpetological assemblages of tropical forests is very complicated. Squamate reptiles inhabit different altitudes in the poly-dominant primary forests, i.e. different types of vegetation from small bushes and small woods to the canopy of the highest belt of this forest. Most squamates present in the fauna of Vietnam are species with arboreal adaptations, belonging to the families of Agamidae, Gekkonidae, Dibamidae, Scincidae, Varanidae, snakes of the families of Natricidae, Colubridae, Lamprophiidae, Elapidae, Viperidae.

It is necessary to remark the seasonal changes of the type of belt occupied by species and its association with the physiological cycle of the animals. It can be explained by examples of arboreal agamids (*Acanthosaura crucigera*) from the southern and central Annam mountains. During the dry and cool winter season it goes down to the ground demonstrating terrestrial mode of life and even "hibernation" under the trunks of the falling trees. The females of the arboreal *Acanthosaura capra* in the same regions of the tropical forests go down to the ground to lay eggs.

The complicated spatial structure of primary tropical forests with five layers of vegetation (ferns: 0-2 m; bush: 2-8m; undercrown: 8-15; canopy: 20-34; overcrown: 40-50 m and above) is optimal for high species richness and coexistence of closely related species with similar ecological requirements. The number of sympatric species is rather high and reaches 8 species of *Elaphe*, 5 species of *Boia*, 10 species of arboreal agamids.

The development of different morphological adaptations to arboreal life in different squamates and the origin of different groups of arboreal lizards and snakes of Vietnam is discussed.

Does frugivore diversity influence seed dispersal and seedling establishment of fruiting plants?

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Seed dispersal plays an important role in the regeneration and conservation of ecosystems. To address the question whether a reduced frugivore diversity due to anthropogenic (e.g. habitat fragmentation), ecological or historical processes

affects seed dispersal and seedling establishment of fruiting plants, we compared seed dispersal in two tree species of the genus *Commiphora* in two areas with different frugivore diversity, South Africa and Madagascar. South Africa has a high frugivore diversity comparable to other continents, Madagascar is strikingly depauperate. In both areas, tree visitation rates, seed handling and crop removal rates were quantified by tree observations. Fruit production and dispersal rates were quantified using fruit traps. Seedlings were mapped along transects, the spatial distribution of adult trees was measured using the T²-method. Trees in South Africa were visited by 13 bird species with Crowned Hornbills (*Tockus alboterminatus*) being the main visitors (29,9%) and dispersers (43,1%). In Madagascar, trees were visited by four bird species with Lesser Vasa Parrot (*Coracopsis nigra*) as main visitor (57,5%) and disperser (100%). Total dispersal rates in South Africa were considerably higher than in Madagascar (66,3% versus 9,0%) which was due to differences in frugivore diversity and especially handling behavior. Whereas in South Africa most visitors dispersed seeds by swallowing them (11 of 13), in Madagascar dispersal only took place when parrots left with a seed in their beak. Correlating with different seed dispersal rates, seedling distributions in South Africa showed a higher density away from the closest *Commiphora* tree. Furthermore, adult trees in South Africa were uniformly distributed, in Madagascar they showed a clumped distribution. Results show that regional differences in frugivore diversity and especially seed handling behavior have a strong impact on the seed dispersal rates of a plant, on seedling establishment and possibility on the spatial distribution of adult trees.

The Ichthyological Section of the ZFMK: Topics of research in biodiversity

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Biodiversity initiatives have hitherto tended to focus on terrestrial systems or, when aquatic systems are targeted, on coral reefs or wetlands. Freshwater ecosystems have not attracted much attention but they are under serious threats and are disappearing as a result of human induced impacts. Many poor communities take their benefit from the high economic value of freshwater biodiversity. Therefore, mechanisms forming the species diversity in freshwater ecosystems are the main research topics in the fish section of the ZFMK.

At the moment, the ZFMK has six projects on freshwater biodiversity. They are:

- Biodiversity and perspectives for sustainable utilization of fish resources in mountain regions of Central Vietnam.
- Changes of distribution and ecological adaptation of fish species in the massively disturbed ecosystem of the river Rhine.
- Molecular phylogeny of Cichlids in the coastal drainages of Tanzania and Kenya.
- Patterns of ecology and intra-fluvial migrations of the European Eel *Anguilla anguilla*.

- Phylogeny and distribution of rainforest restricted Cyprinodontiforms and Cichlids in West- and Central Africa.
- Postglacial migration patterns and speciation of the european cold-stenotherm freshwater fishes in the *Cottus gobio*-group.

Influence of tree species and habitat structure on the canopy beetle fauna in Semliki Forest, Uganda

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The arthropod fauna of 24 trees belonging to *Cynometra alexandri* (Caesalpiniaceae), *Ficus capensis* (Moraceae), and *Elaeis guineensis* (Arecaceae), was collected in Semliki Forest, a lowland rain forest in Uganda, using insecticidal fogging technique. Altogether 51410 arthropods, including 2377 beetles were found, the latter were additionally assigned to 487 morphospecies. Chrysomelidae, Curculionidae, Corylophidae and Staphylinidae were the most abundant taxa. Alpha-diversity of the beetle fauna, calculated by several indices and rarefaction, is very similar on the different tree species. Beta-diversity was expressed by Morisita-Horn-Indices. Faunal overlap among conspecific trees was significantly higher than between different tree species. Specialisation of beetles on the distinct tree species, and the influence of microhabitats on the distribution patterns are discussed.

Geckos milk honeydew produced by Cicada in Madagascar

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During studies in a West Madagascan dry forest, data on the behaviour and feeding ecology of geckos were systematically collected, mainly from *Phelsuma madagascariensis kochi* in the rainy season from December 1996 to March 1997. In this time mutual correlations between geckos and cicada have been observed, which are described here for the first time. Daygecko species of the genus *Phelsuma* and *Lygodactylus* as well as the nocturnal gecko *Homopholis sakalava* show a specific cicada milking behaviour in which cicada excrete a drop of honeydew as an interspecific key stimulus reaction. Milking behaviour was also observed in *Phelsuma abotti* on Nosy Be in northern Madagascar. Similar mutual behaviour patterns are well known between ants and green flies but have not been reported for vertebrates yet. Cicada of the family Flatidae feed on the phloem fluids of different tree species in Madagascar. The insects pierce the bark of the trunk; here the geckos seek for the insects and stimulate the honeydew secretion.

During the dry season in August, 1998, the individually known 'cicada trees' were checked again but neither milking behaviour nor cicadas could be observed during that period (Knogge pers. comm.). Possibly the use of honeydew compensates a seasonal lack of floral nectar or tree gums during the rainy season.

An exact analysis of the ingredients of the honeydew and their concentrations is still outstanding. In greenflies, previous investigations on honeydew show a consistence of 90-95% of carbohydrates in its dry substance and 0,2-1,8% nitrogen in form of amino acids and amids.

Trophobiotic relationships lead to particular secretion behaviour. For example, Homoptera living associated with ants display an interspecific communication pattern at which the honeydew secretion of the green flies is induced by open jaws and soft stroking movements of the antennae of the ants. According to these observations of key stimuli, the similar gecko-cicada relationship must be regarded as a developmental trophobiotic stage. As these insects usually occur locally in high densities the high sugar concentrations of their excretions may cause severe problems by reducing their mobility and breathing abilities. The reported disposal of their excrements obviously is an advantage for the cicada. It has never been observed that geckos mistook cicada for prey.

Morphological age-dimorphism and its eco-ethological consequences illustrated for the White-tailed Hawk (*Buteo albicaudatus*)^{*}

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The White-tailed Hawk (*Buteo albicaudatus*) lives in southern Venezuela in isolated savannas within the tropical rain forest. In the course of a study of the "Surumoni Project", clear differences in the flight silhouettes of juvenile and adult White-tailed Hawks were noticed. This was confirmed by measurements of studied skins, which revealed significant differences at the hawks' wings and tails. The wings of juvenile hawks are characterized by their greater length, larger Kipp's distance, deeper notches and longer alulae. In addition, the juvenile hawks have longer and more rounded tails and a lower wing load than the adults. Initial observations in November/December 1997 and 1998 showed that these morphological differences are reflected in the hawks' hunting behavior and habitat selection. Significant differences in the hawks' hunting behavior, especially regarding 6 distinct hunting modes as well as flight altitude, were also recorded. The lighter juvenile hawks used only 2 flight styles (gliding and soaring, equally frequent) at a lower altitude, whereas adults used 4 different flight styles (gliding, soaring, hovering and flap gliding, in descending order) at a higher altitude. With respect to habitat selection, juveniles tend to prefer the hilly grass savannah, as opposed to the wooded cliffs and plains of the savannah preferred by the adults.

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Centers of endemic terrestrial vertebrates in Colombia: a methodological approach

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The distribution of endemic species is increasingly used as a tool for the identification of key sites for nature conservation in a global scale. Additionally, endemic species are important indicators for the evaluation of the resilience and complexity of a regional landscape.

More than 450 species of terrestrial vertebrates are endemic to Colombia, another 300 are also common to neighboring countries (Guzman 1997, preliminary data). Although most of these species are well-known since the last century, there are still doubts concerning their taxonomic identity and some details of their population ecology, the risk of extinction and their real distribution.

Nevertheless, if we use the existing data on Colombia's fauna, it is possible to define 42 areas in northern, western and Andean regions, which show that various centers of endemism exist in Colombia.

This investigation intends to supply informations on the zoogeography of Colombia by reviewing all records on endemic terrestrial vertebrates of Colombia, scattered all over the world. In a first step, the informations on amphibians, reptiles, birds and mammals of Colombia and the influence of similar geomorphological, ecological and historical processes on their endemicity are analysed.

An „ENDEMIC SPECIES CATALOGUE“ will be compiled, specifying distribution, density maps and taxonomy. Scientific and photographic informations will be obtained from published accounts, additionally supported by data from museums and universities in Colombia, the USA and Europe. A "BIOGEOGRAPHICAL ANALYSIS" of the centers of endemism will result in a comparison of their natural conditions as regional unities in Colombia and its vicinity. As a case study, the present situation of habitats in a center of endemism in the Sierra Nevada de Santa Marta will be evaluated and the ecological viability of an endemic population will be analysed (by GIS).

This work has been guided since 1995 by the University of Stuttgart and the Museum of Natural History in Stuttgart

Mammalian biogeography of the Japanese Archipelago and rodent communities size structure

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The Japanese archipelago is located at the eastern coast of Asia and encloses more than 3900 islands of widely different areas, ranging from less than one sq. km to more than 230 000 sq. km. All these islands remained isolated from the adjacent Asiatic mainland since the last sea lowering during Quaternary, and the extant mammalian fauna is assumed to originate from Miocene.

The distribution pattern of terrestrial mammal species in Japan is in accordance with the first prediction of the MacArthur & Wilson theory, i.e. the diversity on islands is highly related to the island size. However, this study reveals the importance of non-equilibrium effects. At a large scale, the current distribution of mammals in Japan seems to be due to selective post-glacial extinction processes. A large proportion of the Japanese mammals is endemic, and extinctions were not balanced by the colonization of species from the Asiatic mainland. Additionally, we show the importance of inter-islands dispersal processes, in particular from larger islands to smaller ones. Deep marine channels between islands affect as well the proportion of endemic species present on islands as the inter-island colonization.

Additionally, we investigated the intraspecific patterns of morphology of the size variations among muridae from Japan, using the size of the lower incisor as an estimate of body size. Different geographical trends can be demonstrated, where the size was mainly affected by a latitudinal gradient as well as by island area.

Generally, small mammals tend to evolve gigantism on islands. However, many recent studies reveal the importance of competitive interactions between sympatric species that influence the community size structure. We used three different approaches to test the influence of interspecific competition on murid community structure. We can not present any regular size structure. However, evolution on islands seems to reduce competition between species by minimizing size overlaps between them. These results may indicate that interspecific competition is higher on island communities, when compared to mainland ones, mainly due to limited resources on island environments.

The real biodiversity is inside

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Parasites are often suggested to be the most prevalent organisms on earth and parasitism itself is considered to be the most common lifestyle within eukaryotic organisms. Most biological knowledge therefore stems from studying the nonparasitic minority of species and knowledge about parasites of wild living vertebrates is more or less fragmentary. Coccidia (*sensu stricto*) are usually termed protozoan apicomplexan parasites of the family Eimeriidae. Members of this family parasitise all vertebrate groups and some of them are also known from invertebrates. Due to their high host specificity, coccidia represent a highly diversified group of protozoans. Probably the only estimation of coccidian diversity is that published by Levine in 1965, expecting more than $2,5 \times 10^6$ species just within the single genus *Eimeria*.

Although data on host specificity of coccidian species of reptiles are lacking, the specificity on the level of host species or genus can be expected. Our comparison of the diversity of African reptiles and their coccidia leads to the evidence that these hosts lack coccidia (probably similar to the situation in other groups of parasites).

The number of species of reptiles inhabiting the African continent, reported by Welch (Herpetology of Africa, 1982) is about 990 (surely deeply underestimate) and so far, there are only 33 coccidia of the family Eimeriidae reported from reptile hosts (Agamidae: 2; Boidae: 1; Chamaeleonidae: 1; Colubridae: 5; Cordylidae: 1; Elapidae: 1; Gekkonidae: 5; Lacertidae: 4; Scincidae: 8; Varanidae: 1; Viperidae: 5). The only encouraging is the fact that 10 of these species were described within the last decade. Coccidian diversity is documented on results of our research on East African members of the family Chamaeleonidae, which revealed 6 new species (3 *Eimeria* and 3 *Isospora*) within 8 examined chameleon species.

Main reasons for simultaneous research on vertebrates and their parasites are the following: a) speciation of parasites and their hosts is approximately simultaneous and data on parasite phylogeny could elucidate the phylogeny of hosts (and *vice versa*); b) some of coccidian species are pathogenic and can represent a serious threat for programs of captive or semi-captive propagation of endangered vertebrate taxa; c) some of the coccidia of wildlife represent potential pathogens of domestic animals and man.

The amphibia of an isolated archipelago: the Eastern Arc forests, Tanzania

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The Eastern Arc Mountains, from Teita Hills, Kenya to Udzungwas Mountains in Tanzania, have a natural vegetation of moist evergreen forest from low altitude up to the limit of forest vegetation at about 2400 m a.s.l.

Based on studies of amphibians, the zoogeography of these forests – as a sequence of forest islands in a sea of savanna – is described. Due to a very long isolation the fauna in these forests is unique. In spite of the minute size of the forests, the level of endemism for those species living in the moist forest is 100% when compared with the central forest block in Africa, and very high when compared with the other forests in Eastern and Southern Africa.

The fauna of these forests is described, their uniqueness discussed and comparison made with other groups of animals, and with forests on isolated mountains elsewhere in Eastern and Southern Africa.

The forests on the Eastern Arc are small and dwindle fast. Conservation of the forest flora and fauna is the most urgent conservation priority in Africa.

The *Alcolapia* Species-Flock (Teleostei: Cichlidae) of Lakes Natron and Magadi, Kenya and Tanzania: Another Piece in the Puzzle of Cichlid Evolution?

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Recently a small species flock of tilapiine cichlids (‘Soda tilapias’) was collected from East Africa, including *Alcolapia alcalicus* (Hilgendorf, 1905), formerly known as *Oreochromis a. alcalicus*, from Lake Natron, Tanzania and Kenya, and *A. grahami* (Boulenger, 1912), formerly known as *O. a. grahami*, from lake Magadi, Kenya. Two further, morphologically highly deviating species were described, *Alcolapia ndalalani* (Seegers & Tichy, 1999) and *A. latilabris* (Seegers & Tichy, 1999). Geological studies have shown that Magadi and Natron are remnants of a former paleolake, called ‘Orolonga’, which split 8,000 - 9,000 years bp into the modern lakes. Molecular and fossil data indicate that the ‘Soda tilapias’ and especially the species from Lake Natron radiated after the separation of the lakes. The different morphotypes resemble species in head morphology and oral dentition known from lakes Malawi (mbunas: rock dwelling species) and Tanganyika, and especially *A. latilabris* looks like some morphotypes believed to be ‘perfectly adapted’ to the rocky shores of these lakes. A molecular study of 61 specimens shows only small differences between 18 haplotypes found, thus indicating the monophyly of the ‘Soda tilapias’. The sequence data clearly represent a gene tree and not a species tree. An outgroup comparison with the four morphologically closest and geographically nearest *Oreochromis* species shows a close relationship of all ‘Soda tilapias’ while *Oreochromis* is relatively more distantly related. We therefore consider *Alcolapia*, formerly a subgenus of *Oreochromis*, as a valid genus. Since the ‘Soda tilapias’ are not directly related to the cichlid flocks from lakes Malawi and Tanganyika this would imply that the striking similarity in head morphology and dentition evolved at least three times. However, we assume that these similarities are not the result of independent and at least threefold adaptive radiations, especially since the rocky shores of the other two lakes are not present in Lake Natron. Instead, we believe that the morphotypes are caused by ‘re-awakening’ of early acquired developmental mechanisms by genes leading to similar morphotypes as a result of a relatively high mutation pressure in Lake Natron as indicated by the high number of haplotypes.

Comparative adaptive behaviour of Derby Eland in the zoo of the Wildlife College, Garoua and the Benoue National Park Zoo

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Study period: June, July, August, September 1986

Classification: Phylum: Vertebrata; Class: Mammalia; Order: Artiodactyla; family: Bovidae; genus: *Taurotragus* (Crandell, 1964)

Five races were recognized by Allen (1939). There are two outstanding species, namely the Common Eland (*Taurotragus oryx*) and the Giant Eland (*Taurotragus derbianus*), the former being smaller in size and the latter being more robust and having larger horns.

Distribution: *Taurotragus derbianus* is found from Senegal eastwards across Nigeria, Northern Equatorial Guinea, and North Eastern Congo to Sudan. *Taurotragus oryx* is found in the plain areas of Africa from the Cape north to Angola and Kenya, although in the South it now exists only in preserves.

Findings:

1. Feeding: The eland is more a browser than a grazer in both localities. The food intake had a large moisture content, high percentage of crude protein and high percentage of nitrogen free extract. The five major food types eaten by the Eland in the Garoua zoo had high digestibles on dry matter basis. The nutrient composition of food types of Eland in both zones was very similar. That in the school zoo ate more water yam in the dry season than in the wet season, more vegetation in the wet season than in the dry season and it drank similar quantities of water in both seasons.

2. Time budgeting: The female eland rested more than the male in the school zoo and fed less than the male. In the Benoue environment there was no real difference in the activities of the male and female eland. The most prominent daily activities in both zones were feeding, resting and walking; while fighting and courtship were the least. The Eland in the school zoo fed most in the afternoon, rested most in the evening and walked most in the morning. In the Benoue environment it fed most in the evening, rested most in the morning and walked most in the evening. Climatic conditions greatly influenced their activities.

Phylogeny of the anuran genus *Mantella* from Madagascar

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Malagasy poison frogs of the genus *Mantella* (Ranidae: Mantellinae) are among the most prominent and attractive amphibians from Madagascar. Studies on systematics and distribution of *Mantella* can contribute important data to assess the conservational status of species. This is of special interest since large numbers of specimens are yearly exported for pet trade.

We combined a systematic revision of the genus with phylogenetic studies using osteological, morphological, bioacoustical, caryological and allozyme characters. All data sets agree in defining several species groups within the genus. Recent molecular studies carried out by M. Veith and C. Schäfer (Mainz University) corroborated the monophyly of most of these. Geographic distribution of species within species groups is largely allopatric or parapatric; all cases of syntopy regard species of different groups. Nei's genetic distance ranges from 0.04 to 0.4 within species groups and from 0.18 to 0.75 between species of different groups. *Mantella laevis* and the *M. betsileo* group are considered as the most basal lineages within the genus. *M. madagascariensis* and *M. baroni*, which are extremely similar to each other by dorsal colouration, are no sister species and belong to different species groups, indicating that Müllerian mimicry could partly be responsible for the pattern similarity. These examples show that the phylogeny of *Mantella* can contribute important new aspects both to the still poorly understood patterns of Madagascan biogeography, and to the general evolutionary mechanisms related to aposematism.

Distribution patterns and specificity of Chrysomelids (Coleoptera) in central African forests

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Chrysomelidae were collected in forests of Kivu, Rwanda, and predominately Uganda, ranging from lowland rain forests (670 m a.s.l.) to upper montane forests (2950 m a.s.l.). Data were collected during dry and rainy season. In Budongo Forest, Uganda, trees were fogged in secondary and adjacent primary forest plots. Chrysomelid abundance is strongly influenced by foraging ants in the tree crown. Faunal overlap of leaf beetles is lower on conspecific trees between primary and secondary forest than on different tree species in one of these forest types. The community structure of chrysomelids shows high differences between seasons in Budongo Forest, while the fauna shows much higher similarities between different forests during dry season. Especially small Alticinae were highly abundant in all forests investigated during dry season. These beetles were possibly aggregated along a gradient of humidity in the tree crowns. Data underline low specificity to plant species, and high influence of predation and abiotic factors on the composition of arboreal tropical chrysomelid communities.

Lessons on evolutionary processes from an unwanted experiment in a tropical fish community

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Lacustrine East-African cichlid fishes provide outstanding examples of isolated vertebrate communities in the tropics. In spite of differences in age, origin and limnology, each of the three great lakes (Tanganyika, Malawi and Victoria) contains several hundreds of endemic fish species of the family cichlidae. Though the cichlid flocks in these lakes evolved independently, there is a considerable anatomical and ecological resemblance between species from different lakes. The diversity in Lake Tanganyika is greatest due to its older age and the polyphyletic origin of its cichlid species.

The monophyletic flock of Lake Victoria, comprising more than 500 species, is extraordinarily young since 12 400 years ago the lake was dry. The fast evolution of the cichlids in Lake Victoria can be explained by disruptive sexual selection upon male coloration allowing speciation even in sympatry. The cichlid bauplan apparently facilitated subsequent adaptive radiation into virtually all available habitats and food sources of the lake. The anatomical difference between closely related sympatric species is generally small, sometimes even smaller than environmentally induced intraspecific differences in allopatry or allochrony. The young species are genetically isolated by premating barriers which can be disturbed by environmental changes.

In the 1980s approximately 200 cichlid species vanished from Lake Victoria, particularly in the sublittoral and offshore waters which cover by far the greatest

part of the lake. The main cause of this decline was an explosive population increase of Nile perch, a huge predator introduced into the lake in the 1950s. Concomitant eutrophication and algal blooms resulted in a decrease of water transparency and of oxygen concentrations which in turn may have contributed to a further decline of the cichlids. However, unexpectedly, recent surveys demonstrated the recovery of some species, while closely related, ecologically similar species fail to cope with the new ecosystem. The dramatic perturbations in Lake Victoria provide us with natural experiments on the ecology and evolution of vertebrate communities in the tropics and warn us for the vulnerability of these unique ecosystems to human interference.

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